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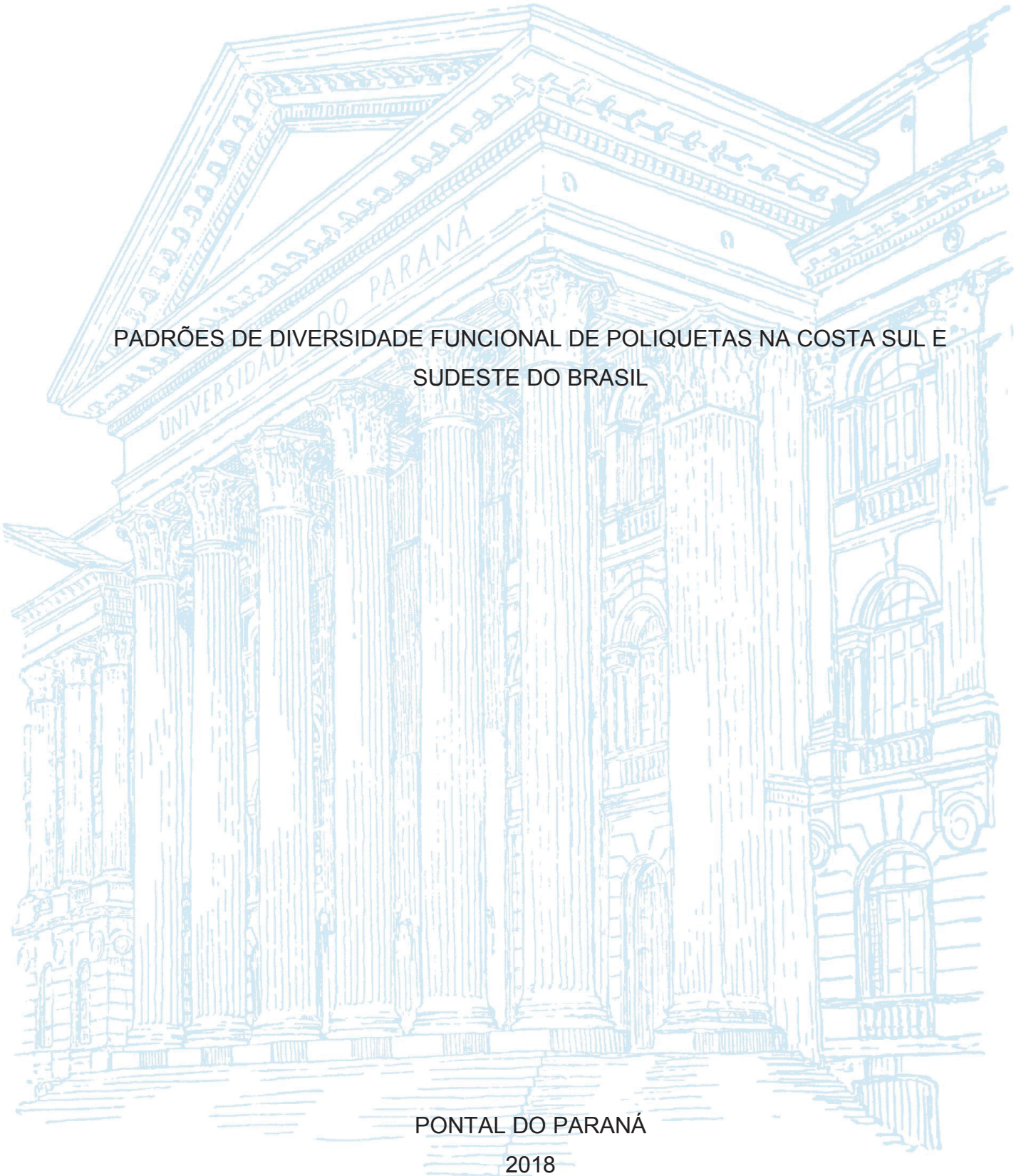

PADRÕES DE DIVERSIDADE FUNCIONAL DE POLIQUETAS NA COSTA SUL E SUDESTE DO BRASIL

PONTAL DO PARANÁ

2018

BARBARA CAROLINA GARCIA GIMENEZ

PADRÕES DE DIVERSIDADE FUNCIONAL DE POLIQUETAS NA COSTA SUL E SUDESTE DO BRASIL

Tese apresentada ao curso de Pós-Graduação em Sistemas Costeiros e Oceânicos, Setor de Ciências da Terra, Universidade Federal do Paraná, como requisito parcial à obtenção do título de Doutor em Sistemas Costeiros e Oceânicos.

Orientador: Prof. Dr. Paulo da Cunha Lana

Coorientador: Prof. Dr. Daivid Mouillot

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DEDICATÓRIA

Em tempos de crise política e econômica refletindo-se demasiadamente na educação, dedico esse trabalho ao povo brasileiro que banca as bolsas de pós-graduação com seus impostos.

"Droit devant soi on ne peut pas aller bien loin..."

A. de Saint-Exupéry - Le Petit Prince

"Quando a gente anda sempre para frente, não pode mesmo ir longe..."

A. de Saint-Exupéry – O Pequeno Príncipe

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APRESENTAÇÃO DA TESE

Esta tese inclui uma Introdução Geral, três capítulos na forma de artigos e Considerações Finais. A Introdução Geral apresenta a fundamentação teórica e os problemas ecológicos que motivaram a elaboração do trabalho. Cada capítulo representa um manuscrito científico elaborado com base nas normas da revista em que será submetido, embora algumas adaptações tenham sido feitas para manter a coesão da tese. O primeiro capítulo, fruto da minha qualificação de doutorado, foi redigido para publicação na revista *Journal of Sea Research* e intitula-se "Trait-based approaches to assess macrofaunal function in coastal environments: a critical review". É uma revisão teórica sobre as abordagens metodológicas mais utilizadas na ecologia funcional de comunidades e ecossistemas, a partir de estudos focados no macrobentos marinho. O segundo capítulo, "How the functional diversity of polychaete assemblages is affected by sediment parameters in subtropical estuarine systems?", é uma avaliação dos padrões de diversidade funcional das assembleias de poliquetas em sistemas estuarinos subtropicais da costa sul e sudeste do Brasil. Para esse manuscrito contei com dados fornecidos pelo professor Mauricio Camargo e seus alunos. Foi redigido pra submissão à revista *Estuarine, Coastal and Shelf Science*. No terceiro e último capítulo da tese, intitulado "Investigating functional redundancy in polychaete assemblages of the South Brazil Shelf Large Marine Ecosystem (SBSLME)", utilizei dados extraídos da NONATObase (http://nonatobase.ufsc.br/) para avaliar níveis de redundância funcional das assembleias de poliquetas em ambientes de plataforma e estuarinos, no *South Brazil Shelf Large Marine Ecosystem (SBSLME)*. Parte deste trabalho foi desenvolvido durante meu doutorado sanduíche na Université de Montpellier (Montpellier, França), sob supervisão do Prof. Dr. Daivid Mouillot. Esse terceiro manuscrito está redigido no formato da revista *Marine Ecology Progress Series*. Por fim, a seção Considerações Finais sumariza os principais resultados e conclusões da tese.

RESUMO

Há muitos métodos para medir a diversidade funcional das espécies e avaliar o papel das comunidades ou assembleias no funcionamento dos ecossistemas. Avaliações da diversidade ou redundância funcionais de invertebrados bênticos possibilitam uma melhor compreensão dos ambientes de alta variabilidade ambiental, como os estuários. Com o objetivo de fornecer uma visão integrada do tema, no primeiro capítulo foram revisadas as principais abordagens baseadas em atributos funcionais utilizadas para avaliar a função da macrofauna bêntica em sedimentos não consolidados. No segundo capítulo, verificou-se que a diversidade funcional de poliquetas é baixa em estuários da costa sul e sudeste do Brasil e influenciada principalmente pelos nitrogênio total e tamanho médio dos grãos. Os parâmetros sedimentares, sobretudo os orgânicos (i.e., nitrogênio, fósforo, carbono e matéria orgânica) atuam principalmente sobre a composição funcional das assembleias, sugerindo que atributos funcionais estão relacionados com processos ecológicos estruturadores, como ciclagem de nutrientes, produção secundária e fluxo de energia. Por fim, no terceiro capítulo, foi observado que a redundância funcional de poliquetas é baixa em ambientes de plataforma e em fundos estuarinos tropicais, embora seja maior nesses últimos, onde a complexidade ambiental sustenta um número maior de táxons compartilhando atributos funcionais similares (i.e., desempenhando funções ecológicas semelhantes). Embora ainda haja muito a ser estabelecido e testado antes de se aplicar amplamente as abordagens revisadas e utilizadas nessa tese, nossos resultados indicam que essas métricas podem avaliar satisfatoriamente a função do macrobentos em ecossistemas costeiros. Para uma maior validação de abordagens funcionais é necessário, no entanto, que mais estudos sobre a biodiversidade de invertebrados marinhos incluam o componente funcional da diversidade.

Palavras-chave: Assembleias bênticas; Abordagens baseadas em atributos funcionais; Parâmetros do sedimento; Estuários; Diversidade funcional; Redundância funcional; Plataforma continental.

ABSTRACT

Many methods are currently available to measure the functional diversity of species and to assess the role of communities or assemblages in ecosystem functioning. Functional diversity or redundancy evaluations of benthic invertebrates provide a better understanding of environments with high environmental variability, such as estuaries. With the aim to provide a more integrative view on the subject, in the first chapter we critically reviewed the most popular trait-based approaches used to evaluate the macrobenthic role in soft-bottom sediments. In the second chapter, we indicated that the functional diversity of polychaetes is low in estuaries of the southern and southeastern Brazilian coast, and influenced mainly by the total nitrogen and average grain size. Sedimentary parameters, especially organic ones (i.e., nitrogen, phosphorus, carbon and organic matter) act mainly on the functional composition of the assemblages, suggesting that functional attributes are related to structuring ecological processes, such as nutrient cycling, secondary production and energy flow. Finally, in the third chapter, we showed that the functional redundancy of polychaetes is low in tropical continental shelf and estuarine environments, but higher in the latter, where environmental complexity supports a larger number of taxa sharing similar functional attributes (i.e., performing similar ecological functions). Although there is still much to be established and tested before widely applying the approaches reviewed and used in this thesis, our results indicate that these metrics can satisfactorily evaluate macrobenthic function in coastal ecosystems. Further validation of functional approaches requires, however, that more studies on marine invertebrate biodiversity include the functional component of diversity.

Keywords: Benthic assemblages; Trait-based approaches; Sediment parameters; Estuaries; Functional diversity; Functional redundancy; Continental shelf.

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INTRODUÇÃO GERAL

O CONTEXTO TEÓRICO DO TRABALHO DE TESE

Segundo Rahbek (2005), um padrão é a percepção da relação entre várias observações da natureza que sugerem uma configuração particular das propriedades do sistema examinado, refletindo-se na maneira com que esta configuração é retratada estatística e graficamente. Compreender os processos que regulam e modulam os padrões de variação da biodiversidade está entre os objetivos mais antigos e desafiadores da ecologia (Hawkins, 2001; Martínez-Meyer et al., 2013). A diversidade é em última análise definida por esses processos, como é o caso das interações bióticas e abióticas que impõem restrições à biodiversidade, que atuam como filtros ambientais sobre o *pool* de espécies, levando à formação dos diferentes tipos de padrões de ocorrência, distribuição e função (Götzenberger et al., 2012; Münkemüller et al., 2012). Os filtros, por sua vez, são fatores determinantes na estruturação das comunidades biológicas, ao agirem de forma seletiva sobre as espécies (Pavoine and Bonsall, 2011; Münkemüller et al., 2012).

Quase dois séculos de pesquisas têm mostrado a ubiquidade de padrões espaciais da diversidade (e.g., do gradiente latitudinal da biodiversidade) com ênfase tradicional na diversidade taxonômica (Jablonski et al., 2006; Berke et al., 2014; Fine, 2015). Para medi-la, a riqueza de espécies e os índices de diversidade têm sido as medidas mais comumente utilizadas, tanto em trabalhos locais como regionais. No entanto, a diversidade biológica não é composta unicamente pela faceta taxonômica e, além das espécies, incorpora componentes como as características funcionais e as unidades evolutivas, que são mensuráveis em diferentes escalas de tempo e espaço (Pavoine and Bonsall, 2011). Assim, estabelecer padrões levando em conta esses outros componentes da biodiversidade é um requisito igualmente importante para a compreensão dos processos estruturadores de padrões locais e regionais, e para a previsão de respostas bióticas frente às mudanças ambientais (Stevens et al., 2003;

Swenson et al., 2012).

O uso de abordagens que considerem as distintas facetas da diversidade (i.e., taxonômica, funcional e filogenética) tem se mostrado útil para uma melhor compreensão de como a biodiversidade se distribui e varia no espaço, elucidando os fatores que explicam a composição das comunidades e a estruturação das assembleias (Cadotte et al., 2013; Monnet et al., 2014). A diversidade funcional é uma métrica da biodiversidade que estima o tipo e o valor de atributos funcionais mensuráveis no nível de indivíduo e que tenham impacto no *fitness* do organismo (Tilman, 2001). Medir a diversidade funcional significa quantificar qualquer característica morfológica, fisiológica, comportamental ou fenológica de uma espécie, que possa afetar ou condicionar o funcionamento das comunidades ou ecossistemas como um todo (Violle et al., 2007; Luck et al., 2013). De fato, os distintos atributos funcionais que compõem uma comunidade podem assegurar uma série de processos ecossistêmicos, como produtividade, ciclagem de nutrientes e resposta a distúrbios (Mouillot et al., 2011; Naeem et al., 2012; Bender et al., 2016).

A diversidade funcional pode ser utilizada de maneira combinada com a riqueza de espécies para testar os efeitos de gradientes ambientais ou de perturbações sobre a estrutura das comunidades (Gerisch et al., 2012; Luck et al., 2013; Mouillot et al., 2013). A diminuição da diversidade funcional concomitante com o aumento da riqueza ao longo de um gradiente de perturbação, por exemplo, pode indicar a perda de espécies que possuam combinações únicas de atributos funcionais (i.e., espécies raras e especialistas) e aumento desproporcional de espécies que compartilham uma maior quantidade de atributos entre si (i.e., espécies comuns e generalistas) (Gerisch et al., 2012). Dessa forma, as estratégias para mapeamento da biodiversidade para fins de conservação e compreensão de processos geradores também devem se concentrar nas distintas características funcionais que atuam nos processos e no funcionamento ecossistêmico (Diniz-Filho et al., 2013).

Parte fundamental dessa discussão, a redundância funcional é uma característica das comunidades que incorpora o conceito da similaridade funcional entre as espécies. Sob essa perspectiva, diferentes espécies desempenham o mesmo papel funcional em um ecossistema, garantindo elevada redundância funcional no ambiente (Fonseca and Ganade, 2001). Assim, é comum assumir que, se a redundância funcional for alta, mudanças na diversidade de espécies não afetarão o funcionamento ecossistêmico. Em outras palavras, quanto mais espécies constituírem os tipos funcionais de um dado ecossistema, menor impacto haverá na continuidade das funções ecológicas diante de uma rápida perda de espécies (Loreau, 2004; Mouillot et al., 2014). Portanto, a redundância funcional é importante sobretudo para a conservação dos ecossistemas, uma vez que a sobreposição de funções realizadas pode garantir resistência ou resiliência frente a distúrbios (Rosenfeld, 2002; Elliott et al., 2007).

Muitos métodos já foram propostos para quantificar a faceta funcional da biodiversidade (Petchey and Gaston, 2006; Mouchet et al., 2010), sendo alguns deles mais simples e diretos, como a alocação de espécies em guildas ou grupos funcionais (Blondel, 2003). Contudo, o conceito de diversidade funcional incorpora diferentes dimensões (e.g., riqueza, equitabilidade, divergência) que podem ser expressas através de índices uni e multivariados relativamente complexos (Cadotte, 2011). Na sua maioria, essas medidas baseiam-se na construção de um espaço multidimensional para descrever a forma como este é preenchido pelas espécies da comunidade, levando em conta as particularidades de cada dimensão (Villéger et al., 2008). Outras técnicas, como a análise de atributos biológicos (Bremner et al., 2003), descrevem padrões de variação dos atributos ao longo de gradientes espaciais ou temporais por meio de ordenações multivariadas. Todas as métricas têm suas vantagens e limitações e sua escolha deve ser cautelosa, levando em conta os objetivos do trabalho, bem como a comunidade e/ou ecossistema avaliado.

Embora a necessidade de descrever e entender padrões de diversidade seja hoje

notoriamente reconhecida, a maioria dos estudos nesse campo têm utilizado vertebrados terrestres e plantas superiores como ferramenta de investigação, enquanto organismos menores e sistemas aquáticos ainda recebem pouca atenção (Heino, 2011). Esforços recentes têm buscado um melhor entendimento dos fatores que condicionam os padrões espaciais observados nos ecossistemas marinhos (Webb et al., 2009), onde modificações impostas pela perda de habitats, alterações hidrodinâmicas, poluição e mudanças climáticas têm ocorrido sem documentação rigorosa e afetado diretamente os serviços ecossistêmicos (Jackson, 2001; Danovaro et al. 2008; Feng et al. 2018).

A macrofauna bêntica fornece bens e presta serviços ecossistêmicos marinhos importantes, como as trocas de energia e massa entre a coluna de água e o sedimento, a bioturbação e a ciclagem de nutrientes (van der Linden et al., 2017; Wouters et al., 2018). Dentre os organismos que constituem o macrobentos, os poliquetas normalmente contribuem com elevada diversidade e abundância, principalmente em áreas costeiras (e.g., praias e estuários) e em ambientes de plataforma continental (Hutchings, 1998; Narayanaswamy et al., 2005; Levin and Dayton, 2009). Os padrões de diversidade de poliquetas são bastante representativos, tendendo a refletir os padrões de toda a macrofauna (Hughes et al., 2009). Por essa razão, eles têm sido comumente utilizados como *proxies* ou substitutos das comunidades bênticas marinhas para a investigação de padrões ecológicos e, como é o caso específico desta tese, para a avaliação de padrões de diversidade funcional. Esses organismos exibem elevado polimorfismo em seus atributos funcionais e, consequentemente, alta diversidade funcional potencial, constituindo portanto um excelente objeto de estudo no âmbito de ecologia funcional (Martin and Bastida 2006, Otegui et al. 2016, van der Linden et al. 2017).

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CAPÍTULO 1

TRAIT-BASED APPROACHES TO ASSESS MACROFAUNAL FUNCTION IN COASTAL ENVIRONMENTS: A CRITICAL REVIEW[1]

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A B S T R A C T

Over the last decade, trait-based approaches have been increasingly used to assess the relationship between benthic diversity and ecosystem functioning. To deal with a burgeoning literature and to provide a more integrative view on the subject, we have reviewed the most popular trait-based approaches currently used to evaluate the macrobenthic role in marine soft-sediments. A critical analysis of the methods was done, highlighting their main advantages and limitations. The techniques include uni- and multivariate metrics, such as benthic quality indices, functional diversity indices, and Biological Trait Analysis (BTA). Our results indicate that multivariate indices have been widely used, but their results are highly case-specific and hardly comparable across studies. Conversely, BTA allows for more objective comparisons among similar environments in relation to multivariate indices, by providing a clear picture of how trait attributes change across samples or environmental gradients. Even though there is much to be established and tested before widely applying trait-based approaches to assess macrobenthic function, these metrics are indeed an informative way to describe community structure and can shed new light on the role of macrofauna in modulating or regulating benthic systems.

Keywords: Functional diversity; Traits; Macrobenthic role; Multivariate measures.

1. Introduction

It is well known that macrobenthic species play a relevant role in the functioning of marine systems. They are secondary producers in marine food webs and a food source for higher trophic levels (Cusson and Bourget, 2005; Bolam and Eggleton, 2014). The macrofauna participates in important marine ecological processes, such as benthic-pelagic coupling (i.e. the exchange of energy and mass between the water column and the sediment), bioturbation, and nutrient cycling (Griffiths et al., 2017; van der Linden et al., 2017; Wouters et al., 2018). Local disturbance in the sediment matrix by macrobenthic organisms may modulate ecosystem processes, changing the vertical structure of the layers and modifying particle distribution and stability (Kristensen et al., 2012). These small-scale disturbances mediated by so-called bioturbators play an important role in maintaining a mosaic of patches in different successional stages, promoting local heterogeneity and favoring increased beta and gamma diversities (Thrush and Dayton, 2002; Natálio et al., 2017). Bioturbation also produces biogeochemical changes, enables aeration and stimulates aerobic microbial activity (Lohrer et al., 2004; Mermillod-Blondin, 2011). The changes in sediment redox conditions have significant implications for the cycling of nitrogen, sulfur, and organic carbon compounds in marine systems (Mermillod-Blondin, 2011).

The capacity of macrobenthic species to alter sediment characteristics is directly related to their behavior and morphological traits. Epifaunal species can affect the sediment surface by selective deposit feeding, despite their limited capacity to disturb the subsurface sediment matrix (Alvarez et al., 2013). Conversely, sediment diffusers can disrupt the sediment matrix in all directions, destabilizing the substrate and increasing nutrient release (Kristensen et al., 2012). Tube and gallery-dwellers not only promote more profound oxygenation of the sediment, but also, can change sediment microtopography (Berke, 2012;

Kristensen et al., 2012). Bioirrigators promote water flow through the sediment matrix, resulting in increased nutrient release (Chennu et al., 2015). Upward and downward conveyors transport material out or down into the sediment and may directly regulate the release and burial of organic matter in the sediment matrix (Kristensen et al., 2012). Besides, animal size greatly influences their capacity to change the substrate (Solan et al., 2004; Queirós et al. 2013). Considering the differences in bioturbation capacities among macrobenthic species, changes in assemblage structure have clear implications for sediment-related processes mediated by the fauna.

Natural and anthropogenic disturbances are among the most relevant controlling drivers of macrobenthic structure in marine sedimentary environments (Harris, 2014; van der Linden et al., 2016a). Bottom trawling and dredging, for example, can eliminate habitat-forming organisms and remove large macrobenthic bioturbators from extensive areas in the seafloor, resulting in habitat losses and noticeable reductions in environmental heterogeneity (Thrush and Dayton, 2002; Muntadas et al., 2014; Veiga et al., 2017). The increasing pressure of human-driven large-scale disturbances on coastal seascapes, such as climate change and overfishing, generates concern among researchers and marine managers about the consequences of benthic biodiversity loss on the benthic processes, ecosystem functions and services (Halpern et al., 2015). Analytical tools that integrate information about the functional traits of macrobenthic species to assess the relationship between species composition and community function are thus valuable to predict benthic functioning in case of small- or large-scale disturbances (Mouillot et al., 2013; Gusmao et al., 2016). Trait-based ecology has grown strong in the past years, and recent research has produced relevant information in both aquatic and terrestrial systems (Gerisch et al., 2012; Schirmel and Buchholz, 2013; D'Agata et al., 2014; Gusmao et al., 2016). To deal with this burgeoning literature and provide a more integrative view on the subject, in this paper we have reviewed the most popular trait-based

approaches used to evaluate the macrobenthic role in marine soft-sediments. Specifically, our aims were (1) to assess which methods have been most used to assess macrofaunal function in coastal environments; (2) to conduct a critical analysis of the currently used techniques, highlighting their main advantages and limitations; and (3) identify the main challenges and precautions prior to using trait-based approaches to assess the macrobenthic function. A critical summary of the revised methods is presented in Table 1. We have also provided an R script with trait-based approaches to assess macrofaunal function (Appendix A).

2. Evaluating macrobenthic function in soft sediments

Functional diversity is the component of biodiversity associated to ecosystem properties and processes (Tilman, 2001; Violle et al., 2007). Despite the notable accumulation of functional diversity studies in recent decades, there is still no consensus on the conceptual definitions of the term (Petchey and Gaston, 2006; Laureto et al., 2015; Schmera et al., 2017). Anyway, measuring functional diversity means quantifying the variety of species functions within an ecosystem, which is directly related to the species traits (behavioral, morphological or physiological) that somehow affect ecosystem functioning (Violle et al., 2007, 2012; Luck et al., 2013). Species traits are any characteristics that can be observed and measured at the individual level and which are necessarily linked to organismal performance (Díaz and Cabido, 2001). A functional trait necessarily assumes different values or categories, often referred to as attributes (Violle et al., 2007). However, not all traits that affect an organism performance are equally relevant to altering or maintaining ecosystem functions (Mlambo, 2014). To consider a trait as genuinely functional, its attributes need to be directly or indirectly related to the given ecosystem functions (Mlambo, 2014). For example, in soft-bottom environments, macrobenthic traits associated with movement through the sediment

and production of mucus and biogenic structures are considered functional since they can directly affect the stability, nutrient cycling, and input of organic matter and oxygen of the sediment (Reise, 2002; Widdows and Brinsley, 2002; Bremner et al., 2006a).

The idea that macrobenthic species vary in their capacity to modify the sedimentary environment is not new, and a variety of methods have been applied to measure the benthic function. Some of these methodologies were explicitly designed for marine soft benthos, such as AMBI (Borja et al., 2000) and bioturbation potential (Solan et al., 2004; Birchenough et al., 2012). Other techniques, such as functional diversity indices and multivariate trait analysis (often being referred to as Biological Trait Analysis − BTA, as first described by Bremner et al., 2003) have a wide range of applications and have been applied to assess the macrobenthic function in coastal environments. Trait-based approaches to assess ecosystem function can be affected by the traits chosen by a given researcher and may be highly influenced by the study aims and the quantity/quality of available trait information (Bremner et al., 2003, 2006b; van der Linden et al., 2012; Mlambo, 2014).

2.1. Biotic indices: measuring environmental status

Biotic indices are metrics that represent the responses of benthic soft-bottom communities to natural and anthropogenic changes. They integrate multiple types of information about species composition and derive a single value that characterizes the environmental state of an ecosystem (Borja et al., 2000; Salas et al., 2006; Basatnia et al., 2015). Although environmental quality indices have not been developed to address the functional diversity or benthic function, they are based on the functional structure of communities since they account for information about species' life history traits (Bonada et al., 2006). In this way, biotic indices can be understood as estimates based on certain

functional aspects of the community to evaluate the quality of an ecosystem. These indices assume that communities reflect their environment and biotic interactions, and that organisms have varying responses and levels of tolerance to different habitat structures and pollution (i.e. different combinations of functional response traits).

According to Salas et al. (2006), benthic quality indices can be classified into five main groups: (1) indices based on indicator species, which consider the presence/absence of certain indicator species (e.g. AMBI Index, BENTIX; Borja et al., 2000; Simboura and Zenetos, 2002); (2) indices based on ecological strategies, focused on the life history traits of organisms (e.g. index of r/K strategies, Polychaeta/Amphipoda Index; Gesteira and Dauvin, 2000; De Boer et al., 2001); (3) indices based on values of specific diversity (e.g. Shannon, Margalef and Simpson diversities; Magurran, 2011); (4) indicators based on biomass or abundance of species (e.g. abundance-biomass curves, sensu Pearson and Rosenberg, 1978); (5) integrative indicators which incorporate multiple sources of information on the benthic assemblages and their environment, and synthetizes the information in a single value (e.g. B-IBI Index, TRIX; Weisberg et al., 1997; Wollenweider et al., 1998).

Although there may be significant loss of information in deriving a single index to describe the condition of an entire community or ecosystem, such routines are considered useful for marine management. Since a single index reduces the complexity of grossly unexplained raw data and can be statistically related to a range of physical, chemical, and biological measures, it may facilitate the interpretation of ecological data for both specialists and non-specialists engaged in ecosystem management and conservation. However, due to the high complexity and diversity of benthic assemblages, the application of single biotic indices to assess a source of disturbance is often restricted to specific systems. Consequently, the efficiency of an index is limited to a geographical context and any application or extrapolation

beyond this context must be done with caution (Dolédec et al., 1999; Borja et al., 2000; Statzner et al., 2001; Salas et al., 2006).

2.2. Bioturbation potential: estimating a specific function of soft sediment assemblages

Bioturbation, i.e. the particle reworking and irrigation of sediment, is a central ecosystem function performed by benthic species in marine environments (Queirós et al., 2013). Bioturbation potential index BPc (Solan et al., 2004; Birchenough et al., 2012) is a quantitative metric developed exclusively for soft-sediment benthos that is an indicator of benthic faunal function on sediment reworking. BPc considers three functional traits recognized as influential in the process of sediment bioturbation: average body size (expressed as body mass), mobility through the sedimentary matrix, and mode of sediment reworking. Species abundance and biomass are also included in quantification, and the index can be calculated for both individual species and entire communities (Birchenough et al., 2012). Furthermore, the bioturbation potential can also be used as an indicator of environmental quality, and for the management of marine benthic ecosystems (Birchenough et al., 2012; Queirós et al., 2013). However, like any other technique, its application requires some precautions. Recent studies reported that BPc may not be a reliable measure of the real bioturbation capacity of some benthic species (Alves et al., 2017; Gogina et al., 2017). Bioturbation potential does not account for intraspecific variability in trait values, intra- and inter-specific interactions, the actual contribution of species/individuals to the bioturbation process, and the effect of other traits that are important for the bioturbation process, such as feeding behavior and vertical distribution (Gogina et al., 2017). Moreover, information regarding macrobenthic species traits is still scarce, which impose significant restrictions to the BPc application in poorly known areas outside Europe.

Table 1. Summary of the most widely used methods for evaluating the marine macrobenthic function in coastal environments, with some recent practical applications.

Method	Original reference(s)	Main advantages	Main limitations	Practical applications evaluating marine macrobenthic function	Quantifies (the effect) of/on what?
Biotic indices		- Very useful for coastal management - Facilitates the interpretation of grossly raw ecological data - Can be statistically related to a range of physical, chemical, and biological measures	- Loss of information in deriving a single index to describe environmental condition - Application is often restricted to specific systems - Efficiency is limited to a geographical context		
AMBI index	Borja et al., 2000			Feebarania et al., 2016 Lopes et al., 2017 Brauko et al., 2015 Asha et al., 2016	Natural and anthropogenic stress Sediment contamination Sewage contamination Eutrophication
BENTIX	Simboura and Zenetos, 2002				
TRIX	Wollenweider et al., 1998				
Bioturbation potential index (BPc)	Solan et al., 2004 Birchenough et al., 2012	- Good indicator of benthic faunal function on sediment reworking - Can also be used as an indicator of environmental quality, and for the management of marine ecosystems	- Not account for intraspecific variability in trait values, intra- and inter-specific interactions, the actual contribution of species/individuals to the bioturbation process, and the effect of feeding behavior and vertical distribution that are important for the bioturbation process	Gogina et al., 2017 Wrede et al., 2017	Ecosystem functioning expressed by bioturbation Biogeochemical processes
Functional groups	Wilson, 1999 Blondel, 2003	- Simple applicability - Enables the quantification of a given ecological process accurately	- Affected by the abundance of numerically dominant species that hinders the detection of subtle patterns	Alexandridis et al., 2017 Murray et al., 2017 Rius et al., 2018	Assembly mechanisms Environmental impacts Metabolic fluxes

		- Very useful in a descriptive context, besides to address ecosystem functioning and assembly mechanisms	- Difficulties in comparing the results from different studies due to the lack of standardized protocols to classify species into functional groups		
Functional diversity indices		- Reflect the various functional facets of communities or ecosystem functioning - Describe aspects of community structure that are not detectable by the conventional indices of taxonomic diversity - Can be statistically related or modeled with environmental variables	- Usage is often restricted to comparative situations - The results can be abstract and difficult to interpret - Indices reflecting the same functional facet may provide opposite results due to differences in the nature of the calculations		
Univariate metrics					
CWM	Garnier et al., 2004	- Useful in analyses of the relationship between a specific functional trait and certain ecosystem function - Provide relevant information on the capacity of the species to modulate an ecosystem process - Identifies dominant traits that may be linked to specific functions within the community (CWM)	- Restricted use, since most ecosystem properties are dependent on multiple types of functional traits - Often considered unattractive measures and replaced by an equivalent multivariate measure	van der Linden et al., 2016a Weigel et al., 2016	Effluents Functional identity
Multivariate metrics					
FD	Petchey and Gaston, 2002	- Focus on different functional attributes of the	- Highly influenced by the methodological decisions	Törnroos et al., 2015	Reductions in richness

RaoQ	Champely and Chessel, 2002 Botta-Dukát, 2005	community - Can express in a simple way an ecological pattern	and availability of trait information - The results can only be	Darr et al., 2014	Salinity gradient
FAD	Schmera et al., 2009 Schleuter et al., 2010	- Allow direct comparison between studied	interpreted in the context of a specific work and can	Dimitriadis and Koutsoubas, 2011	Aquaculture
FRic, FEve, FDiv, and FDis	Villéger et al., 2008 Laliberté and Legendre, 2010	communities	hardly be compared across studies	Dolbeth et al., 2015	Secondary production
Biological traits analysis (BTA)	Statzner et al., 1994 Bremner et al., 2003	- Gathers information on a range of functional traits exhibited by the whole species pool - Allows objective comparisons among similar environments - Provides an informative picture of how traits change across samples or environmental gradients	- The outcome is affected by the traits chosen to perform the analysis - The gaps in the knowledge of species traits can lead less robust results - Not describe potential functions nor identifies dominant traits	Gusmao et al., 2016 Dauvin et al., 2017 Pitacco et al., 2018	Sewage discharges Human pressures Climate changes
RLQ/fourth-corner	Dolédec et al., 1996 Legendre et al., 1997			Piló et al., 2016 Wouters et al., 2018	Metal contamination Latitudinal gradient and regional drivers

2.3. Guilds and functional groups

One of the first and most widely used methods to quantify the functional diversity of communities was based on the classification of species into groups regarding specific traits, called guilds or functional groups (Wilson, 1999; Blondel, 2003). Although some authors consider the terms guild and functional group as synonyms (e.g. Cummins and Klug, 1979; Wilson, 1999; Usseglio-Polatera, 2000; Pla et al., 2012), they actually mean different things. The guild concept refers to mechanisms of resource sharing by species in a competitive context while functional groups are related to the way that species process a resource or other ecological component in the provision of an ecosystem function (Blondel, 2003). However, the actual application of the two concepts in ecological studies is practically the same. Both guilds and functional groups represent a subset of species present in an assemblage that shares a given trait value. For example, all macrobenthic species that feed on sediment deposits are classified as "detritivores" (Tilman, 2001; Norling et al., 2007). Classification of species into functional groups can be done arbitrarily based on the objectives and assumptions of the ecologist, or they can be estimated by a statistical algorithm that classifies species in groups based on the similarity of their trait values, such as cluster analysis (Pla et al., 2012; Bolam and Eggleton, 2014). Theoretically, the number and abundance of species clusters in a community (i.e. the number of functional groups) reflect the complementarity of species in resource use (Petchey et al., 2004), and as such, are considered as a measure of functional diversity (Norling et al., 2007; Pla et al., 2012).

Although the simplicity of this approach may be attractive for most researchers, classifying species in functional groups has certain limitations that should be considered. First, as well as the approaches based on single traits, the variation of functional group abundances across gradients may be highly affected by the abundance of numerically dominant species (e.g.

Gusmão-Junior and Lana, 2015), which hinders the capacity of this approach to detect subtle variation patterns. Second, there is no standardized protocols to classify species into functional groups, which imposes difficulties to comparing results from different studies. Anyway, an organism, population or community exhibit many interrelated traits, and when quantifying ecosystem processes, functional groups can be relevant in ordering functional traits into groups and making the measure of ecosystem processes more accurate. For instance, body size and mobility are traits linked to each other in the quantification of the same process, bioturbation. Thus, the use of functional groups is again becoming increasingly popular in functional ecology because, besides being useful in a descriptive context (Verberk et al., 2013), they can be also efficient to address ecosystem functioning and assembly mechanisms (Dolbeth et al., 2015; Greenfield et al., 2016; Alexandridis et al., 2017, Villnäs et al., 2018).

2.4. Functional diversity indices

Quantifying the range of functions in a community, expressed by the spectra of trait values of its species, is one of the oldest and simplest measurements of functional diversity (Swenson, 2014). These metrics based on continuous values of a certain trait have different abilities to reflect functional aspects of communities or ecosystem functioning. Ideally, an index of functional diversity should describe aspects of community structure that are not detectable by the conventional indices of taxonomic diversity (Villéger et al., 2008). The community-weighted mean trait value (CWM; Garnier et al., 2004) is the most used univariate index (i.e. based on the values of one single trait) in functional ecology. CWM is a good indicator of the expected functional value of a trait in a given community and is calculated through the average of trait values weighted (i.e. multiplied) by the relative abundances of each species (Garnier et al., 2007; Pla et al., 2012). This metric is responsible for defining the dominant trait-categories

in a community, considering the most abundant species to establish ecosystem processes (Ricotta and Moretti 2011). Although the common use of the index is to analyze single traits separately, from the taxa abundance (local × taxa) and functional trait (taxa × traits) matrices, a trait composition matrix at the community level (local × traits) can be constructed through the CWM and then used in an ordination or gradient analysis (e.g. Gimenez and Higuti, 2017). Despite its potential for ecological investigations, few studies on marine benthic diversity have applied the CWM (e.g. Dolbeth et al., 2015; van der Linden et al., 2016a, b; Weigel et al., 2016), which is mostly used by plant ecologists.

There are other univariate indices to quantify functional diversity which describe different aspects of the trait structure of a community, such as functional range (FRR; Mason et al., 2005), univariate functional richness (FRIS; Schleuter et al., 2010), functional regularity (FRO; Mouillot et al., 2005), and univariate functional divergence (FDvar; Mason et al., 2003). In analyses of the relationship between a specific functional trait and certain ecosystem function (e.g. body size and bioturbation), these indices may be useful and provide relevant information on the capacity of the species to modulate an ecosystem process (Schleuter et al., 2010). However, univariate indices have received less attention from ecologists after the advent of multivariate techniques and computing facilities.

Since the capacity of species to modulate certain ecosystem properties may be highly dependent on multiple types of functional traits, ecologists have developed multivariate indices to estimate community functional diversity (Pla et al., 2012). A first group of these metrics is based on dendrograms that describe the species trait similarities in a community. The calculation of a dendrogram-based index starts with a similarity matrix (Fig. 1a-d) based on the functional traits of the species present in a community (Fig. 1e). The functional diversity (FD) of Petchey and Gaston (2002) was the first and most widely used dendrogram-based index. FD estimates the total length of the branches of the dendrogram, which might be highly affected by the chosen

distance measure (e.g. Euclidean, Bray-Curtis) and the grouping method used to construct the dendrogram (Petchey and Gaston, 2002). Several variants of FD have been proposed, which may incorporate information of a species' relative abundance, such as wFD (Pla et al., 2012), and intraspecific trait variability, such as iFD (Cianciaruso et al., 2009), or apply specific routines for the dendrogram construction, such as GFD (Mouchet et al., 2008). The FD of Petchey and Gaston (2002) and its variants are among the most widely used functional diversity indices in functional ecology literature.

Another group of multivariate indices is based on the functional space of communities, i.e. a functional trait hypervolume that describes the trait space occupied by species in a community (Villéger et al., 2008). The functional space is constructed from a similarity matrix based on a species' functional trait values (Fig. 1f). Although the Euclidean distance is commonly used, any similarity index can be employed depending on the type of trait data, that is, if it is continuous (e.g. size), categorical (e.g. type of embryo development: direct or indirect), or both (Laliberté and Legendre, 2010). The distribution of species in the multidimensional functional space can be visualized in ordinations, such as Principal Components Analysis (PCA) or Principal Coordinate Analysis (PcoA; with multiple traits summarized on each axis – Fig. 1f).

Rao's quadratic entropy (RaoQ) is an index based on the functional trait space that measures the functional differences between pairs of species, weighing their relative abundances. This metric is derived from the quadratic entropy theory of Rao (1982) and represents a generalized form of the classic Simpson diversity index (Champely and Chessel, 2002; Botta-Dukát, 2005). RaoQ is considered a measure of functional dissimilarity, a proposed component of functional diversity that quantifies the dispersion and abundance of species in the functional space (Laliberté and Legendre, 2010; Gerisch et al., 2012). It is considered a robust tool to quantify the functional diversity of communities and has been applied in multiple types

of environments, including the marine benthos (e.g. Darr et al., 2014; Gusmao et al., 2016; van der Linden et al., 2012). There are also alternatives to decompose this index into elements of α, β and γ diversity (Ricotta and Szeidl, 2009; Villéger et al., 2012; 2013; Arnan et al., 2016).

Functional Diversity Attribute (FDA) represents a group of functional diversity metrics calculated on the basis of the Euclidean distance of the species in the functional trait space (Schmera et al., 2009; Schleuter et al., 2010). This group includes the indices FAD1, FAD2, and MFAD. FAD1 quantifies different combinations of functional attributes that occur in a community. FAD2 estimates the sum of the distances between pairs of species in the functional trait space. MFAD is an extension of FAD2 that weights species abundance in the calculations (Schmera et al., 2009). Despite the relative number of studies that use these indices (Schmera et al., 2009; Bihn et al., 2010; Dimitriadis and Koutsoubas, 2011), they are considered unattractive due to their high correlation with species richness and the existence of more robust alternatives for the quantification of functional diversity (Mouchet et al., 2010; Pavoine and Bonsall, 2011).

Villéger et al. (2008) proposed three multivariate indices to estimate different aspects of functional diversity: functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv). Unlike the RaoQ and FDA metrics, which are based on similarity matrix, the measures of Villéger et al. (2008) are based on trait values (Mouchet et al., 2010). Thus, FRic measures the total volume of the convex hull that envelopes all the species in the functional trait space (Fig. 2c). Changes in FRic values are related to the appearance or disappearance of species whose functional traits are extreme or unique (i.e. in the vertices of the convex hull). FEve estimates the regularity degree to which species abundance is distributed in trait space by measuring the branches of the shortest minimum spanning tree, weighted by species abundance, which links all the species in the functional trait space (Fig. 2d). Alterations in FEve are associated with a disproportional increase or decrease in abundance in certain parts of the functional space. FDiv calculates how the species diverge from the average distance to the

gravity center of the functional trait space, weighting the species abundance in the calculation (Fig. 2e). Variations in FDiv are related to changes in the abundances of species with extreme or medium trait values (i.e. located in the periphery or the center of the functional trait space). Laliberté and Legendre (2010) proposed a fourth index to quantify Functional Dispersion (FDis). FDis estimates multivariate dispersion of the species in the functional trait space and might also weight species abundances in the calculation (Fig. 2f). FDis is closely related to RaoQ index and sensitive to increase/decrease of species with medium (i.e. located at the center of functional space) or extreme trait values (i.e. located at the periphery of functional space). There are a number of indices that can used as a complement of the above-mentioned indices, such as Functional Specialization (FSpe), which estimates the relative position of species in the functional trait space; and Functional Originality (FOri) that represents the relative isolation of species in the functional trait space (Mouchet et al., 2010; Mason et al., 2013; Mouillot et al., 2013).

Other multivariate measures focus on the relationship between functional diversity and species richness to infer on the functional redundancy of communities (Mayfield et al., 2010). Some proposed indices, such as Functional Redundancy (FR; Fonseca and Ganade 2001), Functional Vulnerability (FV; Bihn et al. 2010), and Functional Over-Redundancy (FOR; Mouillot et al., 2014), have been commonly employed to describe patterns of functional redundancy (Brandl et al., 2016; Micheli et al., 2014; Mouillot et al., 2014). These metrics can be used to estimate the vulnerability of ecosystem functions to disturbances since the functional redundancy of communities is directly related to resilience (Luck et al., 2013). Thus, a community that presents high functional redundancy (i.e. species sharing similar traits) is less likely to lose specific functions driven by species extinction (Loreau, 2004; Mouillot et al., 2014). Recently, Violle et al. (2017) presented metrics for the calculation of functional rarity that integrates the concepts of functional distinctiveness and taxonomic scarcity observed at the

local scale, and functional uniqueness and taxonomic restrictedness at the regional scale. These metrics describe the functional equivalence and the relative abundance/extent of occurrence of a species (or an organism) in the community or the regional pool, respectively.

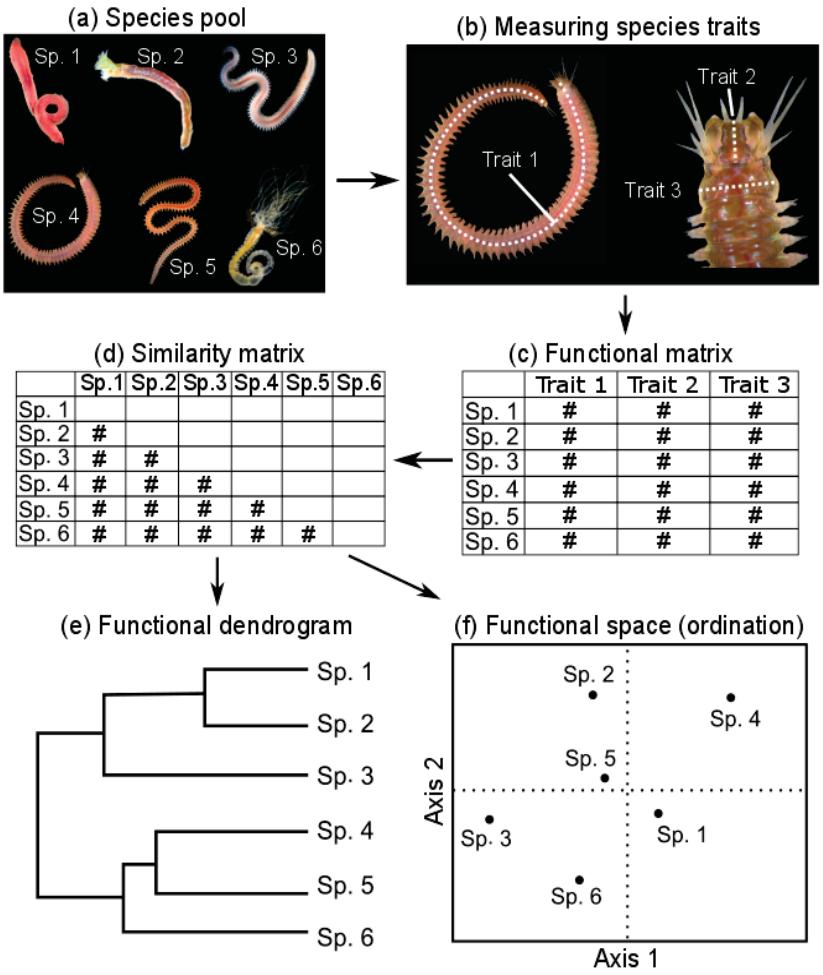

Fig. 1. Logical sequence for the construction of a dendrogram or a functional space representing the species' similarities regarding their functional traits: six species are part of the assemblage (a) and have three traits measured (b): body length (trait 1), prostome length (trait 2), and peristome width (trait 3). Then, the mean values of each trait measured for each species are organized in a functional matrix (c). Subsequently, a similarity matrix relating species according to their trait values is constructed based on a chosen distance measure (d). Finally, one can represent species trait similarities by using cluster analysis to construct a functional dendrogram (e) or a multivariate ordination to represent the functional trait space of the assemblage (f).

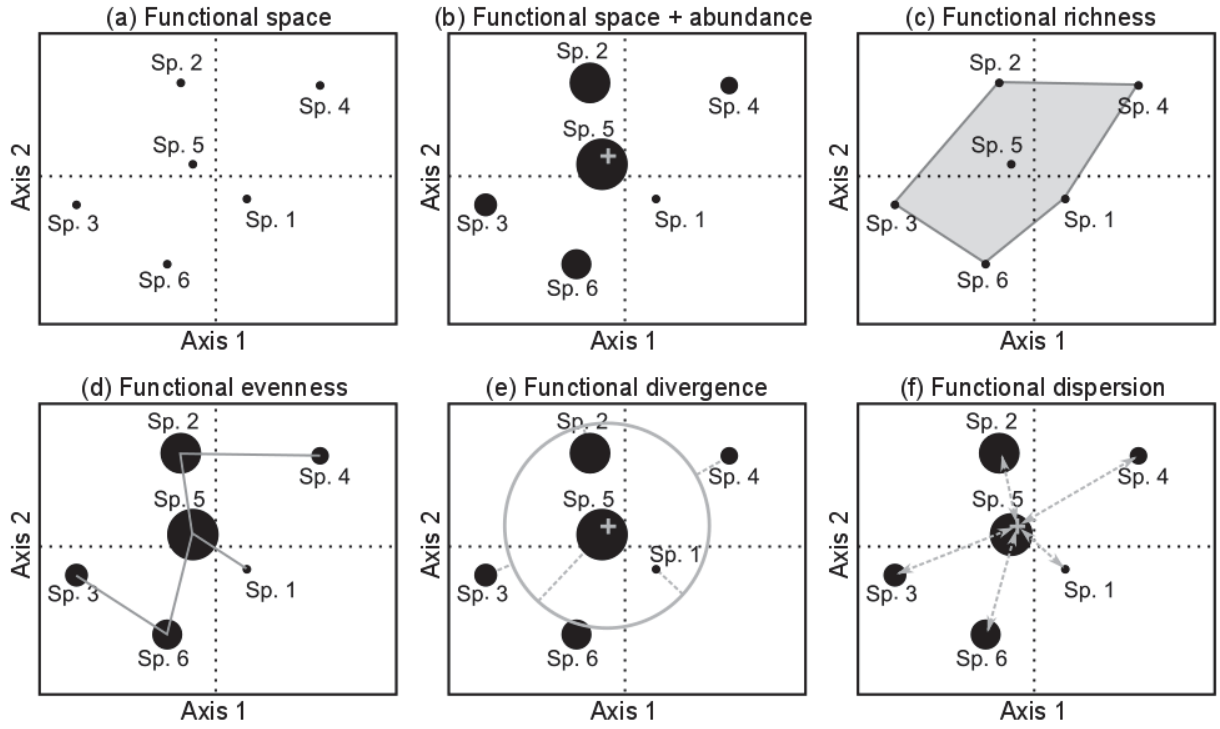

Fig. 2. Representation of the functional diversity components in a multidimensional space, as proposed by Laliberté and Legendre (2010) and adapted from Mouillot et al. (2013). Points represent the position of species in the functional space (defined by the first two axes of an ordination analysis). The size of black circles is proportional to the relative abundance of the species. (a) Distribution of species in the functional space (abundances not accounted); (b) representation of relative abundance in the functional space; (c) Functional Richness (FRic), where the gray polygon represents the convex hull volume; (d) Functional Evenness (FEve); (e) Functional Divergence (FDiv), where the gray circle corresponds to the average distance of the center of gravity in the functional space (gray cross); and (f) Functional Dispersion (FDis), where the arrows depict the distance of each species to the centroid of the ordination.

Functional diversity components can also be used to indicate the relative importance of different processes (assembly rules) in structuring communities. When environmental filtering (i.e. conditions imposed by the environment that limit or allow the establishment of species with certain functional traits) is the dominant process, it is expected that the species within a

community would be functionally similar since they would have functional traits that allow for their establishment in such conditions (Mason et al., 2013; Hedberg et al., 2014). On the other hand, if competition is the dominant interaction that structures a community, it would be expected that species would be highly different in their trait combinations, reflecting niche partitioning (Mason et al., 2007). A third possibility, based on the neutral theory, considers all species as functionally equivalent and that the community structure is a mere random subset of the regional species pool (Hubbell, 2005). Although there are different structuring processes, environmental filters, competition, and stochastic processes are accepted as the most important (Spasojevic and Suding, 2012). These processes can be inferred through the analysis of functional diversity combined with null models (Mason et al., 2007; Spasojevic and Suding, 2012). A null model is a pattern generation procedure designed to infer an ecological or evolutionary process based on the comparison of observed values with randomly generated values (Gotelli and Graves, 1996). Thus, competition would tend to limit species similarity, resulting in communities that are functionally more diverse than expected at random. Environmental filters would promote the opposite pattern, with functionally similar species and lower functional diversity than expected at random. When stochastic processes are significant (or when competition and environmental filters have the same importance), the functional diversity is expected to be similar to that observed in null models (Mouchet et al., 2010).

2.5. Biological Traits Analysis (BTA)

One of the most used approaches to measure the functional diversity of marine benthic assemblages is Biological Traits Analysis (BTA; Bremner et al., 2003), a multivariate method originally proposed for freshwater systems (Chevenet et al., 1994; Statzner et al., 1994; Dolédec et al., 1996). BTA describes the functional trait distribution of biological communities,

incorporating information on the distribution of species' abundances and functional traits across samples or experimental units (Bremner et al., 2006a). Thus, BTA represents changes in trait distribution along environmental gradients, which reflect the relationship among individual traits, environmental factors, and ecosystem functioning – understood here as the maintenance and regulation of ecological processes (Bremner et al., 2006a; Pacheco et al., 2011; van der Linden et al., 2012).

BTA application in marine systems is already quite widespread (e.g. Bremner et al., 2003, 2006a, b; Schratzberger et al., 2007; Cesar and Frid, 2009; Paganelli et al., 2012; van der Linden et al., 2012; Rigolet et al., 2014; van Son et al., 2013). Kokarev et al. (2017) observed the dominance of motile, burrowing, sub-surface deposit-feeders and the absence of sedentary tube-dwelling forms, revealing a distinct functional structure of sampling stations in the Laptev Sea. Dauvin et al. (2017) assessed human impact in the western Mediterranean Sea and identified three different groups of species through BTA: typical species of the environment; indicator species of organically enriched fine sediments; and species which are accessorily found on fine sand. Beauchard et al. (2017) presented a synthesis of the current state-of-the-art use of BTA in the marine environment, reviewing technical applications and pointing out knowledge gaps to guide future researchers.

The BTA uses multivariate ordinations to describe variation patterns in the distribution of the functional traits (Bremner et al., 2006a). Fuzzy Correspondence Analysis (FCA) and Co-Inertia Analysis (CIA) are the most commonly used methods to perform a BTA (Chevenet et al., 1994; Dolédec and Chessel, 1994). Both analyses consider two different matrices: a species abundance (or incidence) per sample matrix, and a functional trait matrix (Fig. 3). The last is constructed using a fuzzy coding procedure based on a score rank system that usually ranges from 0 to 3 and represents the species' association degree to different categories of a functional trait (Chevenet et al., 1994). For example, considering the functional trait "feeding mode," an

herbivorous species would have the score 3 for the category "herbivore"' and 0 for the others, while an omnivorous species would score 1.5 for both the "herbivore" and "carnivore" categories. Then, a third matrix is generated by multiplying the abundance matrix by the trait profiles matrix, which represents trait frequencies weighted by the species abundance in each sample (but see Gayraud et al., 2003 for details of the procedure and associated methodological development). A correspondence analysis based on this "trait per sample" matrix can be used to depict changes in trait compositions along environmental gradients (Fig. 3). In other words, FCA and CIA use CWM and project this on a multidimensional plane, since the CWM values are derived from the same matrix used for BTA.

The traits chosen to perform a BTA can affect the outcome of the analysis and may introduce bias in the interpretation of the results. Although Bremner et al. (2006b) have suggested that BTA becomes more informative when using as many traits as possible, Mlambo (2014) highlighted that the considered functional traits should be carefully chosen since not all of them are actually functional (i.e. some traits would only introduce noise in the analysis). In fact, the BTA used by Bremner can sometimes be somewhat reductive as all traits generally used may not be biological per se. Furthermore, the available information on the biological traits of most macrobenthic species is not precise or still missing.

Other multivariate techniques to perform BTAs also including environmental variables are the RLQ (Dolédec et al., 1996) and fourth-corner analyses (Legendre et al., 1997). RLQ analysis combines the sites-by-environment (or R) matrix, species-by-sites (or L) matrix, and species-by-traits (or Q) matrix to construct the "fourth-corner" (i.e. traits-by-environment) matrix. Both methods can be used together since the RLQ analysis provides a handy graphical summary while fourth-corner analysis tests the significance of the relationship between traits and environmental variables (Dray et al., 2014). Although still poorly used, this method can

provide impressive results in assessing marine macrobenthic trait structure (e.g. Piló et al., 2016; Wouters et al., 2018).

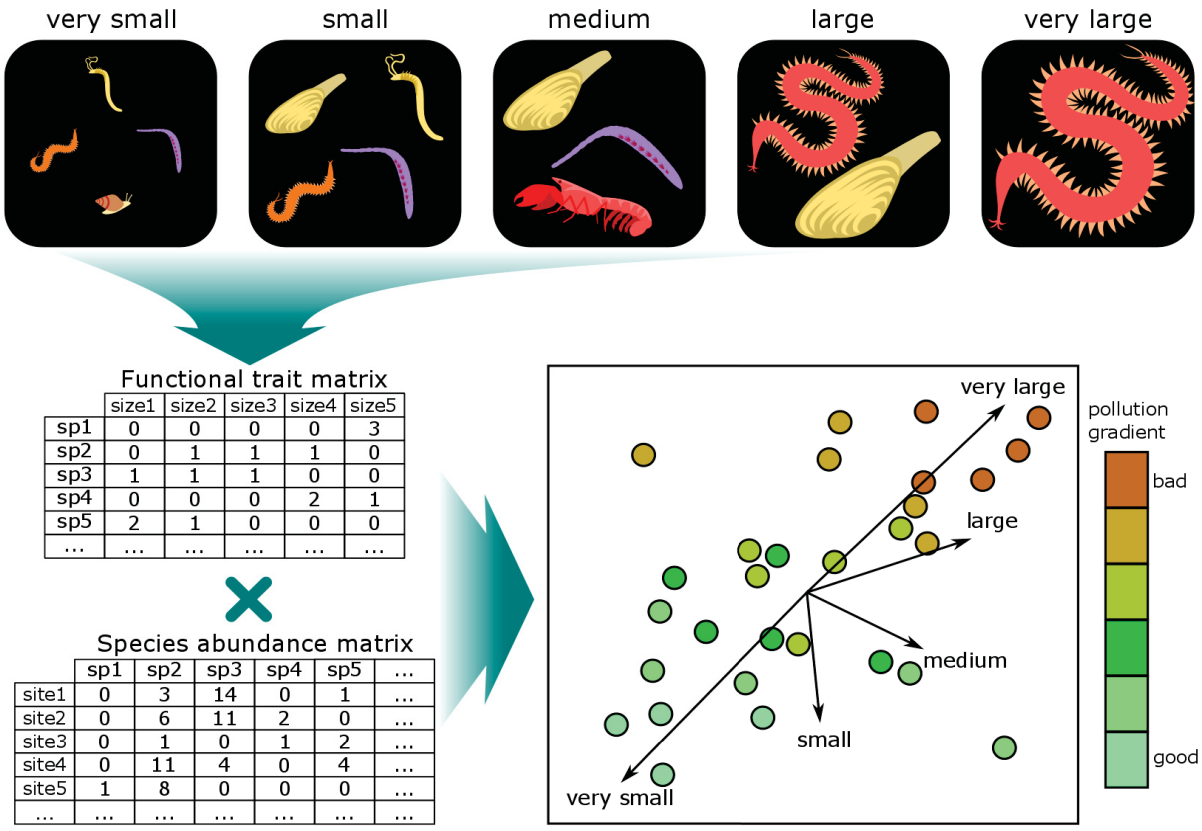

Fig. 3. Diagram depicting the steps to perform a Biological Traits Analysis (BTA) based on the functional trait relative adult size. The trait has five categories (attributes), varying from very small to very big. Fuzzy scores are assigned to each species depending on their association degree to each trait category. By weighing the trait frequencies by the species' abundances in each sampling site, it is possible to represent the variation trends in trait composition across environmental gradients. In the above example, bigger species are associated with polluted sites.

3. Challenges and precautions

Like any other analytical tools, there are many challenges and limitations that should be considered prior to using trait-based approaches to assess the macrobenthic function in marine

systems. Limitations include scarcity and lack of standardization of trait data, lack of empirical studies testing the effect of specific traits on ecosystem processes, lack of standardized methods in analyzing trait data, and the frequently overlooked effect of intra-specific variation of trait attributes.

3.1. Availability and quality of trait data

Detailed information on species' traits is scarce or missing for most benthic organisms, especially in the case of poorly known taxonomic groups and overlooked geographic locations. This is mostly driven by the analytical costs of measuring traits of numerous, but rare or inconspicuous species that thrive in the soft-bottom benthos, which can strongly affect the methodological decisions concerning a trait-based analysis. When reliable information is missing, a common practice is the data extrapolation from the phylogenetic nearest neighbor species (i.e. assuming the similarity between species). However, despite the level of kinship, close species may display different behaviors and life modes, as is the case of polychaetes species of the genus *Nereis*. Recent efforts have managed to organize trait information for specific taxonomic groups. This is the case, for instance, of the collaborative database Polytraits (Faulwetter et al., 2014), which compiles trait information of polychaetes species. Recent reviews have synthesized information on specific functional traits relevant to sediment processes, such as Queirós et al. (2013), which addressed the bioturbation behavior of European benthic species. There are also efforts to compile trait information of specific geographical regions, such as the Marine Macrofauna Genus Trait Handbook (Marine Ecological Surveys Ltd., 2008) focused on benthic organisms occurring in U.K. waters. Other bases compile more general data, namely WoRMS, which includes traits information of all marine species globally, and BIOTIC (MarLIN, 2006), which provides biological traits information of individual benthic

species. Such efforts, however, are still far from the extensive and standardized databases already available for other animals (e.g. FishBase; Froese and Pauly, 2014) and for freshwater organisms (e.g. freshwaterecology.info database; Schmidt-Kloiber and Hering, 2015). Such unified and standardized databases are necessary to allow for the broad application of trait-based approaches to assess benthic systems.

Another limitation is the lack of standardization to describe traits and their associated attributes, as well as the lack of knowledge about how traits interact or relate to the scale on which species use the habitat (Verberk et al., 2013). Different studies that address similar traits frequently diverge on how to describe or measure trait attributes. The trait body size is a good example of such cross-study incongruence. Although some studies consider average weight or body mass as a proxy for body size (e.g. van der Linden et al., 2017), anatomical measures are also often used to describe species' body size (e.g. van der Linden et al., 2012; Rigolet et al., 2014; Gusmao et al., 2016; van der Linden et al., 2016b). For instance, studies that address bivalve assemblages use shell length and height to describe body size (Berke et al., 2014) while body length would be the standard for annelid worms (Wouters et al., 2018). If an ecologist compiles such anatomic-based trait measures of bivalves and worms to analyze the size structure of the entire benthic assemblage, the results will most likely be misleading since the values used for body size cannot be converted at the same proportion to represent organism biomass; thus, giving a biased picture of the trait structure of a benthic assemblage. In an attempt to minimize these discrepancies, van der Linden et al. (2017) considered body mass to categorize polychaetes and mollusks in very small, small, medium, and large. For this, they have considered distinct weight intervals for each taxon, considering the differences across species.

Trying to reduce the limitations in the standardization of available data, Costello et al. (2015) developed a broader vocabulary and a classification of traits, prioritizing those that should be adopted for the marine species already included into the WoRMS database. To avoid

problems related to cross-taxon-trait differences, one could focus on particularly abundant and diverse taxonomic groups. For example, Otegui et al. (2016) proposed a new BTA approach for the functional categorization of polychaetes assemblages based only on morphological traits. Since the polychaetes morphology allows the comparison of both taxonomical and functional approaches, even if not necessarily focused on functional traits, this technique allows for the standardization of existing trait data on unique morphological attributes, reducing subjectivities of the analytical process (Otegui et al., 2016). Wouters et al. (2018) used similar approaches to relate polychaetes trait structure to changes in latitudinal gradients and beach geomorphology. This practice has also been adopted by some databases. However, it is well known that most of the rare species are not yet coded, which can be a problem when addressing some metrics such as functional richness.

3.2. Lack of empiricism linking actual traits to actual processes

Most studies on functional diversity do not present empirical evidence to justify their trait choices when addressing the function of species assemblages. In general, ecologists assume the potential effect of certain traits on a specific ecosystem process and intuitively include them in their analyses. For instance, a researcher interested in assessing the effects of macrobenthic communities on the biogeochemical processes can choose traits that reflect the bioturbation potential, such as body size, type of bioturbation behavior, and mobility through the sediment (e.g. Bolam and Eggleton, 2014). However, studies which addressed the relationship of such morpho-behavioral traits with sediment properties are often restricted to an insufficient number of species (e.g. Michaud et al., 2005; Mermillod-Blondin, 2011) and there is no evidence that multiple species with similar traits would necessarily display the same bioturbation potential. Also, highly bioturbating species are determinant for the nutrient cycling in muddy substrates,

but they lose importance as sediment grain size increases (Mermillod-Blondin and Rosenberg, 2006; Mermillod-Blondin, 2011). These arguments highlight the importance in considering contexts in which a trait is appropriate to address the effects of functional diversity in the environment (or vice versa). Considering the lack of information on the actual functional relevance of used traits, we stress the urgent need of empirical studies on the relationship between functional traits and specific ecosystem properties and processes.

3.3. Overlooked effects of intraspecific variation

Since traits are often collected at the species level, it is assumed that interspecific variability is higher than intraspecific variability, an assumption which was rarely tested. The capacity of organisms to change ecosystem properties and the intensity they interact with other organisms vary along their life (Díaz et al., 2013; Wong and Candolin, 2015). Excluding the obvious functional differences between pelagic larvae and settled adults, benthic organisms can present marked changes in their functional role depending on their development stage. These changes are mostly related to body size (Linse et al., 2006; Eklöf et al., 2017) and diet (Bolnick et al., 2003) and, therefore, have direct implications for local food webs (Layman et al., 2005; Gravel et al., 2016). Different benthic species can also present behavioral changes during certain life stages. For instance, many species of fiddler crabs build sediment structures around their burrows when they become mature (Christy, 1982), changing the microtopography of their sedimentary environment. Trait expression of some species can also change markedly, depending on their location or environmental context (Vaughn, 2010), such as the onuphid worm *Diopatra cuprea*, whose role as an ecosystem engineer changes along a latitudinal gradient (Berke, 2012). Intraspecific variations are determinant to increase the resilience of populations and communities to disturbances, since they can alter species trait rankings along

environmental gradients or at extreme situations (e.g. the limited resource availability), allowing for species persistence even under adverse conditions (Cianciaruso et al., 2009; Jung et al., 2010; Bolnick et al., 2011; Burton et al., 2017). Such examples indicate that intra-specific trait variation can have practical effects on species roles and introduce bias in studies that use trait identities or diversity to assess ecological function. In these cases, multivariate indices may not represent the best way to approach the functional ecology, and univariate metrics should be used instead (Bolnick et al., 2011; Violle et al., 2012). However, the measurement of trait attributes at the individual level is not a logistically viable procedure for most studies.

3.4. Lack of standardized protocols

Although the general interest in trait-based approaches has increased, their application to assess marine benthic assemblages still lacks standardized protocols. This is partially due to the novelty of most methods, which still demand testing before being widely and consistently used to analyze real species communities. Recent studies highlighted that some functional diversity metrics are highly affected by choices taken prior and during calculation (Lefcheck et al., 2015; Maire et al., 2015; Zhu et al., 2017a, b). For instance, multivariate indices can be affected by the number and type of traits chosen for the study, by the availability of detailed information on species' traits, by the distance measure used to construct the functional trait space or dendrogram, by the type of measure used to quantify species' abundances (e.g. density, biomass, or coverage), and by corrections or transformations that can be used when calculating the indices (Leps et al., 2006; Mouchet et al., 2010; Maire et al., 2015; Zhu et al., 2017a). Indeed, there is no standardized methodology for selecting the most appropriate functional traits for a study (Bolam and Eggleton, 2014), but iterative selection or even the hypothesis testing in combination with biological reasoning (Statzner and Bêche, 2010) possibly could reduce the

noise of redundant or irrelevant trait information that could affect the results. All these bias sources indicate a more significant problem ahead. Considering the high degree of subjectivity in the calculation of functional diversity indices (especially those based in multivariate techniques), most of the results derived from such indices can only be interpreted in the light of the choices made by the ecologists and can hardly be compared across studies. Thus, unless benthic ecologists standardize trait choices and make their analytical protocols more objective, other trait-based approaches would represent a better choice to assess the potential function of benthic assemblages. In this context, BTA tends to be less prone to bias since it does not reduce the entire trait structure of an assemblage in an index but describes merely how trait attributes vary along different samples or gradients. Similarly, all the information found in the BTA, can be found when calculating the CWM, but CWM also provides an indication of the dominant traits in the community, something that BTA does less well. In turn, these dominant traits can be used to quantify the rate of ecosystem processes (Vandewalle et al., 2010).

4. Concluding remarks

Although a variety of methods have been proposed in the last decades to assess the relationship between species traits and ecosystem functioning, no technique can be universally applied. Different methods have their strengths and limitations, which depend on the aims of the study and the hypotheses to be tested. There are major challenges that hinder the development of trait-based approaches as an objective way to assess assemblage function, which include lack of trait information, unstandardized terminology, and protocols. Among the most recent methods, the multivariate indices have frequently been used in different types of environments, even though such metrics are highly influenced by the methodological decisions and availability of trait information. Thus, the results derived from such multivariate metrics can only be

interpreted in the context of a specific work and can hardly be compared across studies. Conversely, BTA appears as an alternative to assess functional diversity of marine benthic assemblages because it allows for more objective comparisons among similar environments. Such analyses facilitate the assessment of potential ecological functions of benthic assemblages since they provide a clear picture of how trait attributes change across samples or environmental gradients. BTA may not describe potential functions as specific metric BPc, but it still can be highly useful to explore changes in assemblage structure. CWM has also proved useful as it perceives the shifts in the mean trait values, detecting dominant traits that may be linked to specific functions within the community. Even though there is much to be established and tested before widely applying trait-based approaches to assess the macrobenthic function, the use of BTA, together with classical analysis (i.e. those that have been extensively used in studies of functional ecology, as the functional diversity indices) represents a more informative approach than using species' diversity solely to describe community structure.

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Appendix A. R script: performing trait-based approaches to assess benthic function.

```
## Loading the data
abun <- read.table("abundance.txt", sep=";", header=T, row.names=1)
biom <- read.table("biomass.txt", sep=";", header=T, row.names=1)
fuzzy <- read.table("fuzzy_traits.txt", sep=";", header=T, row.names=1)
trait <- read.table("traits.txt", sep=";", header=T, row.names=1)
envir <- read.table("environment.txt", sep=";", header=T)

## Attaching the necessary packages
## If you don't have a specific package, use the command install.packages
library(ggplot2) #graphical package
library(FD) #to calculate functional diversity indices
## Loading required package: ade4
## Loading required package: ape
## Loading required package: geometry
## Loading required package: magic
## Loading required package: abind
## Loading required package: vegan
## Loading required package: permute
## Loading required package: lattice
## This is vegan 2.4-4
## Attaching package: 'vegan'
## The following object is masked from 'package:ade4':
## cca
library(ade4) #to run Biological Traits Analysis (BTA)
library(vegan) #to run MDS
library(Rmisc) #has functions to expand ggplot2 to plot multiple graphs
## Warning: package 'Rmisc' was built under R version 3.4.3
## Loading required package: plyr
library(ggdendro) #has functions to expand ggplot2 to plot dendrograms
## Warning: package 'ggdendro' was built under R version 3.4.3
library(cluster) #has a function to calculate Gower distance

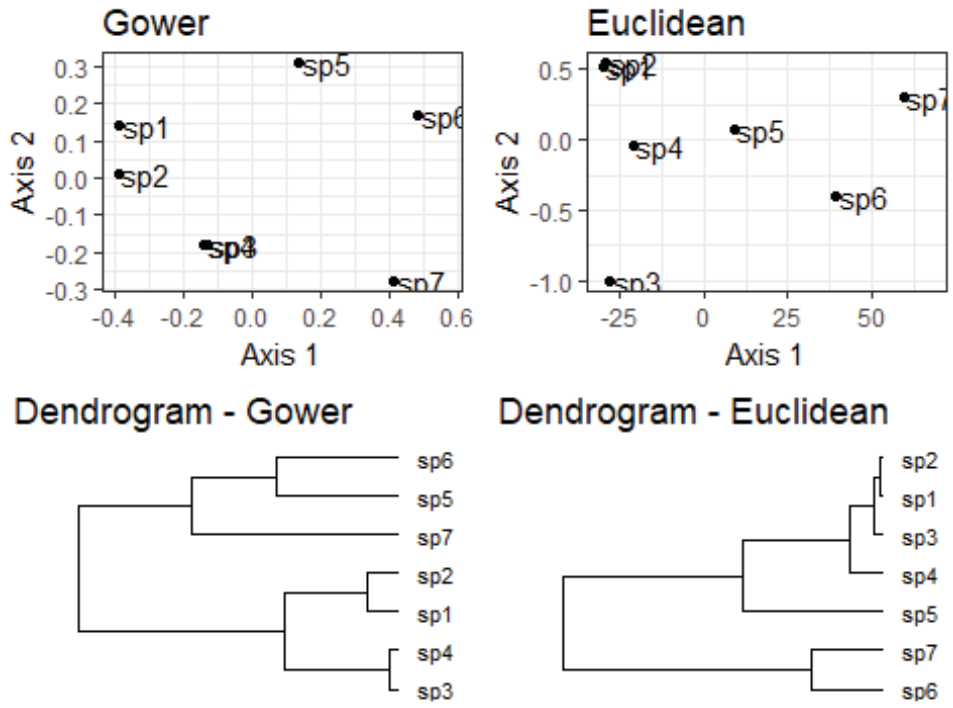
## Let's take a look at the functional trait space
## Since we'll use multiple types of traits, the Gower distance would be the best
choice
gower <- daisy(trait, metric="gower")
g.nMDS <- cmdscale(gower)
g.mod <- hclust(gower)
g.data <- dendro_data(as.dendrogram(g.mod))

## Let's also try only metric traits using Euclidean distances
eucli <- vegdist(trait[,1:3], method="euclidean")
e.nMDS <- cmdscale(eucli)
e.mod <- hclust(eucli)
e.data <- dendro_data(as.dendrogram(e.mod))

## Plotting the functional space
all.spa <- ggplot(as.data.frame(g.nMDS), aes(x=g.nMDS[,1], y=g.nMDS[,2])) +
geom_point() + geom_text(aes(label=row.names(g.nMDS)), nudge_x=0.08) + theme_bw() +
ggtitle("Gower") + xlab("Axis 1") + ylab("Axis 2")
all.den <- ggplot(segment(g.data)) + geom_segment(aes(x = x, y = y, xend = xend,
yend = yend)) + coord_flip() + scale_y_reverse(expand = c(0.2, 0)) + geom_text(data
= g.data$labels, aes(x = x, y = y, label = label), size = 3, hjust = -0.5) +
theme_dendro() + ggtitle("Dendrogram - Gower")
met.spa <- ggplot(as.data.frame(e.nMDS), aes(x=e.nMDS[,1], y=e.nMDS[,2])) +
geom_point() + geom_text(aes(label=row.names(e.nMDS)), nudge_x=8) + theme_bw() +
ggtitle("Euclidean") + xlab("Axis 1") + ylab("Axis 2")
```

```
met.den <- ggplot(segment(e.data)) + geom_segment(aes(x = x, y = y, xend = xend,
yend = yend)) + coord_flip() + scale_y_reverse(expand = c(0.2, 0)) + geom_text(data
= e.data$labels, aes(x = x, y = y, label = label), size = 3, hjust = -0.5) +
theme_dendro() + ggtitle("Dendrogram - Euclidean")

## Let's compare them to see how the representation of the trait space change
multiplot(all.spa, all.den, met.spa, met.den, layout=matrix(1:4, ncol=2))
```




```
## Now we will use the distance measures to calculate multivariate functional
diversity indices
## Let's calculate the indices for Gower and Euclidean distances, using abundances
and biomasses to weight them
fd.gower.abu <- dbFD(gower, abun)

## Species x species distance matrix was not Euclidean. 'sqrt' correction was
applied.
## FRic: Dimensionality reduction was required. The last 4 PCoA axes (out of 6 in
total) were removed.
## FRic: Quality of the reduced-space representation (based on corrected distance
matrix) = 0.795022
## CWM: When 'x' is a distance matrix, CWM cannot be calculated.

fd.gower.bio <- dbFD(gower, biom)

## Species x species distance matrix was not Euclidean. 'sqrt' correction was
applied.
## FRic: Dimensionality reduction was required. The last 4 PCoA axes (out of 6 in
total) were removed.
## FRic: Quality of the reduced-space representation (based on corrected distance
matrix) = 0.795022
## CWM: When 'x' is a distance matrix, CWM cannot be calculated.

fd.eucli.abu <- dbFD(eucli, abun)
```

```
## FRic: Dimensionality reduction was required. The last PCoA axis (out of 3 in
total) was removed.
## FRic: Quality of the reduced-space representation = 0.9999518
## CWM: When 'x' is a distance matrix, CWM cannot be calculated.

fd.eucli.bio <- dbFD(eucli, biom)

## FRic: Dimensionality reduction was required. The last PCoA axis (out of 3 in
total) was removed.
## FRic: Quality of the reduced-space representation = 0.9999518
## CWM: When 'x' is a distance matrix, CWM cannot be calculated.

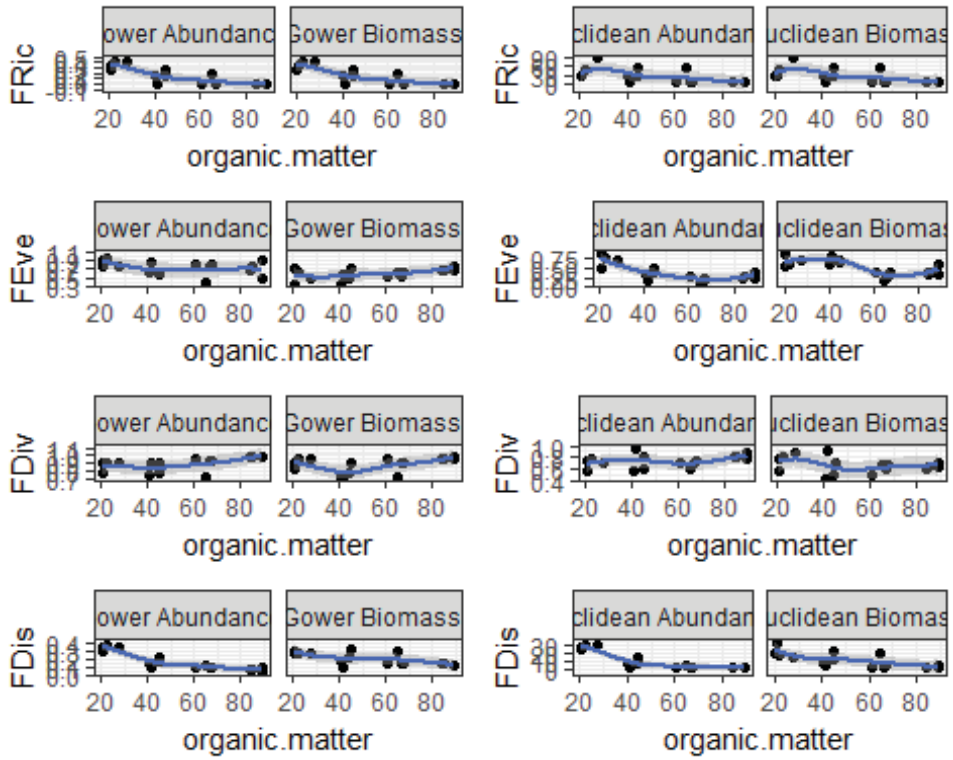
## Now we put everything in the same dataframe
gower.abund <- cbind.data.frame(type=rep("Gower Abundance", 16), envir,
nbsp=fd.gower.abu$nbsp, sing.sp=fd.gower.abu$sing.sp, FRic=fd.gower.abu$FRic,
FEve=fd.gower.abu$FEve, FDiv=fd.gower.abu$FDiv, FDis=fd.gower.abu$FDis,
RaoQ=fd.gower.abu$RaoQ)
gower.biom <- cbind.data.frame(type=rep("Gower Biomass", 16), envir,
nbsp=fd.gower.bio$nbsp, sing.sp=fd.gower.bio$sing.sp, FRic=fd.gower.bio$FRic,
FEve=fd.gower.bio$FEve, FDiv=fd.gower.bio$FDiv, FDis=fd.gower.bio$FDis,
RaoQ=fd.gower.bio$RaoQ)
eucli.abund <- cbind.data.frame(type=rep("Euclidean Abundance", 16), envir,
nbsp=fd.eucli.abu$nbsp, sing.sp=fd.eucli.abu$sing.sp, FRic=fd.eucli.abu$FRic,
FEve=fd.eucli.abu$FEve, FDiv=fd.eucli.abu$FDiv, FDis=fd.eucli.abu$FDis,
RaoQ=fd.eucli.abu$RaoQ)
eucli.biom <- cbind.data.frame(type=rep("Euclidean Biomass", 16), envir,
nbsp=fd.eucli.bio$nbsp, sing.sp=fd.eucli.bio$sing.sp, FRic=fd.eucli.bio$FRic,
FEve=fd.eucli.bio$FEve, FDiv=fd.eucli.bio$FDiv, FDis=fd.eucli.bio$FDis,
RaoQ=fd.eucli.bio$RaoQ)
indices <- rbind.data.frame(gower.abund, gower.biom, eucli.abund, eucli.biom)
row.names(indices) <- c(1:64)

## Let's see how different indices vary along a organic matter gradient
FRic.gower <- ggplot(indices[1:32,], aes(x=organic.matter, y=FRic)) + geom_point() +
facet_grid(.~type) + theme_bw() + stat_smooth()
FRic.eucli <- ggplot(indices[33:64,], aes(x=organic.matter, y=FRic)) + geom_point()
+ facet_grid(.~type) + theme_bw() + stat_smooth()
FEve.gower <- ggplot(indices[1:32,], aes(x=organic.matter, y=FEve)) + geom_point() +
facet_grid(.~type) + theme_bw() + stat_smooth()
FEve.eucli <- ggplot(indices[33:64,], aes(x=organic.matter, y=FEve)) + geom_point()
+ facet_grid(.~type) + theme_bw() + stat_smooth()
FDiv.gower <- ggplot(indices[1:32,], aes(x=organic.matter, y=FDiv)) + geom_point() +
facet_grid(.~type) + theme_bw() + stat_smooth()
FDiv.eucli <- ggplot(indices[33:64,], aes(x=organic.matter, y=FDiv)) + geom_point()
+ facet_grid(.~type) + theme_bw() + stat_smooth()
FDis.gower <- ggplot(indices[1:32,], aes(x=organic.matter, y=FDis)) + geom_point() +
facet_grid(.~type) + theme_bw() + stat_smooth()
FDis.eucli <- ggplot(indices[33:64,], aes(x=organic.matter, y=FDis)) + geom_point()
+ facet_grid(.~type) + theme_bw() + stat_smooth()
multiplot(FRic.gower, FRic.eucli, FEve.gower, FEve.eucli, FDiv.gower, FDiv.eucli,
FDis.gower, FDis.eucli, layout=matrix(1:8, byrow=T, ncol=2))

## `geom_smooth()` using method = 'loess'

## `geom_smooth()` using method = 'loess'
## `geom_smooth()` using method = 'loess'
## `geom_smooth()` using method = 'loess'
## `geom_smooth()` using method = 'loess'
## `geom_smooth()` using method = 'loess'
```

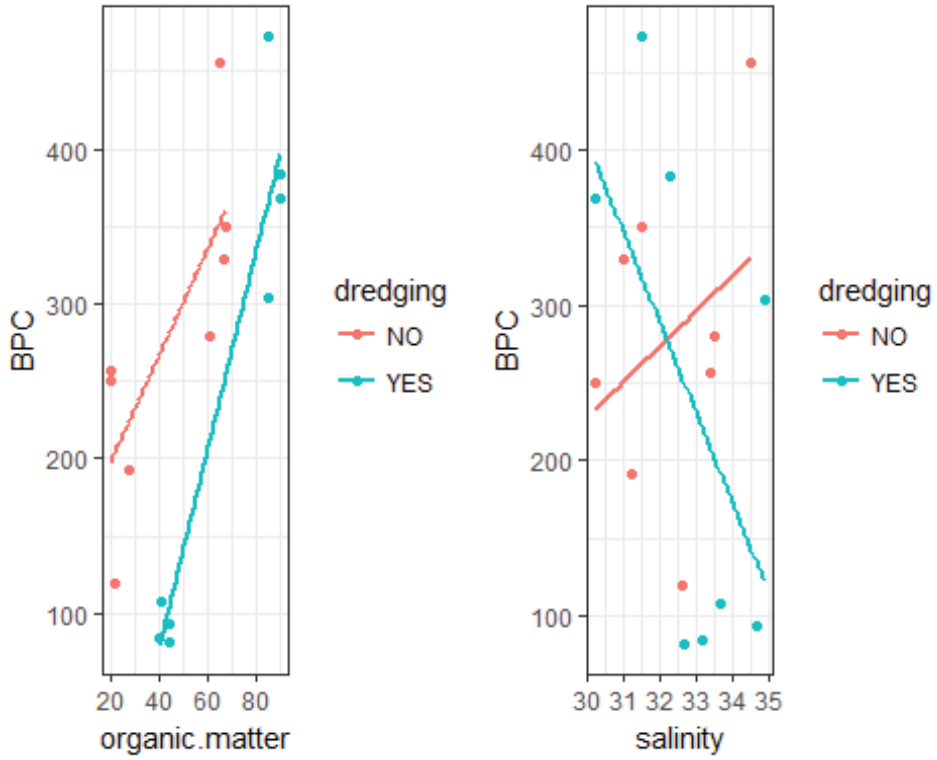
```
## `geom_smooth()` using method = 'loess'
## `geom_smooth()` using method = 'loess'
```




```
## Note: FRic does not weight the abundances/biomasses
## See that some indices, mostly FEve, can change a lot depending on the distace
method and the type of information used as weight

## Let's calculate other indices
## Community Bioturbation Potential (BPc)
## We already have a classification of the traits that we need in the "trait"
dataframe, called "Ri" and "Mi"
## Queirós et al. (2013) present a long list of the bioturbation classification of
European macrozoobenthic species (including Ri and Mi)
ratio <- sqrt(biom/abun)
ratio <- replace(ratio, is.na(ratio), 0)
BPC <- rowSums(ratio*abun*trait$Mi*trait$Ri) #here is the BPc index for each site

## Let's see how it varies along gradients
exBPC <- cbind.data.frame(envir,BPC)
p1 <- ggplot(exBPC, aes(x=organic.matter, y=BPC, col=dredging)) + geom_point() +
stat_smooth(method="lm", se=F) + theme_bw()
p2 <- ggplot(exBPC, aes(x=salinity, y=BPC, col=dredging)) + geom_point() +
stat_smooth(method="lm", se=F) + theme_bw()
multiplot(p1, p2, layout=matrix(1:2, ncol=2))
```




```
## Now let's perform BTAs to see changes in trait compositon
## Let's see how traits categories relate to environmental gradients of organic
matter and salinity
## First, let's use Weighted averages and standard deviations
dev.off()

## null device
##           1

library(SDMTools) #has functions to weighted averages and standard deviations

## Warning: package 'SDMTools' was built under R version 3.4.3

w.trait <- as.matrix(sqrt(abun)) %*% as.matrix(fuzzy) #let's multiply the abundances
by the trait values to created a trait.by.site matrix with trait frequencies
weighted by species abundances. Note we are using squared root abundances to
decrease the effect of any numerically dominant species

## Calculating and putting everything together
wei <- cbind.data.frame(average.sal=apply(w.trait, 2, FUN=wt.mean,
x=envir$salinity),
      average.om=apply(w.trait, 2, FUN=wt.mean, x=envir$organic.matter),
      sd.sal=apply(w.trait, 2, FUN=wt.sd, x=envir$salinity),
      sd.om=apply(w.trait, 2, FUN=wt.sd, x=envir$organic.matter),
      type=c(rep("Size",5), rep("Diet", 4)),
      attr=c(colnames(w.trait)))
wei$attr <- factor(wei$attr, levels=as.character(wei$attr))

## Let's plot the results
p1 <- ggplot(wei, aes(x=attr, y=average.om)) + geom_col() + facet_grid(.~type,
scales="free_x") + geom_errorbar(aes(ymin=average.om-sd.om, ymax=average.om+sd.om,
width=0.1)) + coord_cartesian(ylim=c(0,100)) + ylab("Organic Matter")
p2 <- ggplot(wei, aes(x=attr, y=average.sal)) + geom_col() + facet_grid(.~type,
scales="free_x") + geom_errorbar(aes(ymin=average.sal-sd.sal,
```

```
ymax=average.sal+sd.sal, width=0.1)) + coord_cartesian(ylim=c(25,35)) +
ylab("Salinity")
multiplot(p1, p2, layout=matrix(1:2, ncol=1))

## Fuzzy Correspondence Analysis (FCA)
## It does not allow a direct analysis on the relationship between trait attributes
and environmental variables. But let's see it's results
w.trait <- as.matrix(sqrt(abun)) %*% as.matrix(fuzzy) #let's multiply the abundances
by the trait values to created a trait.by.site matrix with trait frequencies
weighted by species abundances. Note we are using squared root abundances to
decrease the effect of any numerically dominant species
fca <- vegan::cca(w.trait)
plot(fca)

## Now let's do some analysis to directly relate environmental variables and traits

## RLQ and fourth-corner analysis
dev.off()

## null device
##           1

library(ade4)
## Changing the names to make things easier to understand
L <- abun
R <- envir[,2:4]
Q <- fuzzy

## First, let's create a vector with the number of attributies (categories) that our
two traits have
## Body size has 5 and feeding type has 4
categories <- c(5,4)
names(categories) <- c("Size", "Diet")

## Now let's perform a Fuzzy Correspondence Analysis (FCA)
ca <- dudi.coa(L, scannf=F)
hill <- dudi.hillsmith(R, row.w=ca$lw, scannf=F)
prep <- prep.fuzzy.var(Q, categories, row.w=ca$cw)
fca <- dudi.fca(prep, scannf=F, nf=2)

## Ok, we have the things we need to perform a RLQ. Let's do it!
RLQ <- rlq(hill, ca, fca, scannf=F)
summary(RLQ)

## RLQ analysis
##
## Class: rlq dudi
## Call: rlq(dudiR = hill, dudiL = ca, dudiQ = fca, scannf = F)
##
## Total inertia: 0.3051
##
## Eigenvalues:
##      Ax1      Ax2      Ax3
## 0.291046 0.012611 0.001435
##
## Projected inertia (%):
##     Ax1     Ax2     Ax3
## 95.3962  4.1335  0.4702
##
## Cumulative projected inertia (%):
```

```
##     Ax1   Ax1:2   Ax1:3
##   95.40   99.53  100.00
##
##
## Eigenvalues decomposition:
##         eig     covar       sdR       sdQ      corr
## 1 0.2910459 0.5394867 1.2048909 0.8531968 0.5247879
## 2 0.0126111 0.1122992 0.7173276 0.5699735 0.2746656
##
## Inertia & coinertia R (hill):
##     inertia      max     ratio
## 1  1.451762 1.611018 0.9011457
## 12 1.966321 2.595167 0.7576858
##
## Inertia & coinertia Q (hill):
##      inertia       max     ratio
## 1  0.7279448 0.8319585 0.8749773
## 12 1.0528146 1.3168489 0.7994954
##
## Correlation L (ca):
##        corr       max     ratio
## 1 0.5247879 0.7524402 0.6974480
## 2 0.2746656 0.3501433 0.7844377

plot(RLQ) #too much info! Let's separate the results

s.label(RLQ$lR) #site scores
s.arrow(RLQ$l1) #vectors of environmental variables
s.arrow(RLQ$c1) #vectors of trait attributes
s.arrow(RLQ$mQ) #species vectors
barplot(RLQ$eig) #eigenvalues of the ordination

## We can perform non parametric random tests to check the results of our RLQ
analysis
rlq.r <- randtest(RLQ, modeltype=6, nrepet=9999)
rlq.r

## class: krandtest lightkrandtest
## Monte-Carlo tests
## Call: randtest.rlq(xtest = RLQ, nrepet = 9999, modeltype = 6)
##
## Number of tests:   2
##
## Adjustment method for multiple comparisons:   none
## Permutation number:   9999
##      Test       Obs    Std.Obs   Alter Pvalue
## 1 Model 2 0.3050916  7.5640855 greater 0.0001
## 2 Model 4 0.3050916 -0.5965533 greater 0.6132

## Fourth-corner analysis
## It will let us test which environmenal variables best explain changes in trait
compositon
## Might be good to adjust the p-values for multiple comparisons, but we'll let it
now in this simulation
four.cor <- fourthcorner(R, L, Q, modeltype=6, p.adjust.method.G = "none",
p.adjust.method.D = "none", nrepet=9999)
four.cor #the results

## Fourth-corner Statistics
## ------------------------
```

```
## Permutation method  Comb. 2 and 4  ( 9999  permutations)
##
## Adjustment method for multiple comparisons:   none
## call:  fourthcorner(tabR = R, tabL = L, tabQ = Q, modeltype = 6, nrepet = 9999,
p.adjust.method.G = "none", p.adjust.method.D = "none")
##
## ---
##
##                            Test   Stat          Obs     Std.Obs     Alter
## 1  organic.matter / very.small      r  0.309074855  1.56354352 two-sided
## 2        salinity / very.small      r  0.044311114  0.42640528 two-sided
## 3        dredg.NO / very.small Homog.  0.432515300 -0.66751743      less
## 4       dredg.YES / very.small Homog.  0.470361806  0.66701192      less
## 5       organic.matter / small      r -0.022884189  0.09645884 two-sided
## 6             salinity / small      r -0.018619731 -0.25922637 two-sided
## 7             dredg.NO / small Homog.  0.427085133 -0.61762328      less
## 8            dredg.YES / small Homog.  0.547391508  1.41965319      less
## 9      organic.matter / medium      r -0.308132220 -1.00787283 two-sided
## 10           salinity / medium      r -0.038785177 -0.40213890 two-sided
## 11           dredg.NO / medium Homog.  0.558418818  1.05966844      less
## 12          dredg.YES / medium Homog.  0.376240663 -0.35452438      less
## 13        organic.matter / big      r -0.279563947 -0.76418799 two-sided
## 14              salinity / big      r  0.025156763  0.29678381 two-sided
## 15              dredg.NO / big Homog.  0.923511951  1.88186190      less
## 16             dredg.YES / big Homog.  0.056435649 -1.29810717      less
## 17   organic.matter / very.big      r -0.349858994 -1.07719145 two-sided
## 18         salinity / very.big      r -0.065832502 -0.73058490 two-sided
## 19         dredg.NO / very.big Homog.  0.962220492  2.45519660      less
## 20        dredg.YES / very.big Homog.  0.008102772 -2.47644349      less
## 21    organic.matter / deposit      r  0.312637843  1.23109947 two-sided
## 22          salinity / deposit      r  0.031430520  0.36154798 two-sided
## 23          dredg.NO / deposit Homog.  0.605520417  1.60029823      less
## 24         dredg.YES / deposit Homog.  0.342714769 -1.35411265      less
## 25       organic.matter / carn      r -0.464894108 -1.58092916 two-sided
## 26             salinity / carn      r -0.058491787 -0.50768209 two-sided
## 27             dredg.NO / carn Homog.  0.905036426  3.92432650      less
## 28            dredg.YES / carn Homog.  0.051341318 -2.21556314      less
## 29       organic.matter / herb      r -0.431147103 -1.39182630 two-sided
## 30             salinity / herb      r -0.062458173 -0.58554925 two-sided
## 31             dredg.NO / herb Homog.  0.582215321  1.02810461      less
## 32            dredg.YES / herb Homog.  0.405144546  0.11693598      less
## 33     organic.matter / filter      r  0.282732576  1.35736158 two-sided
## 34           salinity / filter      r  0.048619779  0.53387595 two-sided
## 35           dredg.NO / filter Homog.  0.605328316  1.27712391      less
## 36          dredg.YES / filter Homog.  0.394554546  0.03242046      less
##    Pvalue
## 1  0.1384
## 2  0.7028
## 3  0.2824
## 4  0.6406
## 5  0.9273
## 6  0.8145
## 7  0.2738
## 8  0.9594
## 9  0.3976
## 10 0.7036
## 11 0.8509
## 12 0.3463
## 13 0.5568
```

```
## 14 0.7644
## 15 0.9712
## 16 0.2834
## 17 0.3811
## 18 0.4634
## 19      1
## 20 0.0215 *
## 21 0.2553
## 22 0.7238
## 23 0.9464
## 24 0.0973 .
## 25 0.0987 .
## 26 0.6114
## 27      1
## 28 0.0129 *
## 29 0.1688
## 30 0.5591
## 31 0.8239
## 32 0.4753
## 33 0.1888
## 34 0.5945
## 35 0.9014
## 36 0.4567
##
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
## Let's visualize them: blue means negative significant relationships; red means
positive significant relationships
plot(four.cor, alpha = 0.05, stat = "D2") #stat=D2, tests effect of each level of a
categorical variable separately (dredging)
plot(four.cor, alpha = 0.05, stat = "G") #stat=G, tests the global effect of
categorical variables
plot(four.cor, alpha = 0.05, stat = "D") #similar to D2, but using a measure of the
within-group homogeneity

## Now let's test the relationship between RLQ axes and trait attributes
test.rlq.Q <- fourthcorner.rlq(RLQ, modeltype=6,  typetest="Q.axes", nrepet=9999,
p.adjust.method.G="none", p.adjust.method.D="none")
test.rlq.Q
```

```
## Fourth-corner Statistics
## ------------------------
## Permutation method  Comb. 2 and 4  ( 9999  permutations)
##
## Adjustment method for multiple comparisons:   none
## call:  fourthcorner.rlq(xtest = RLQ, nrepet = 9999, modeltype = 6, typetest =
"Q.axes",      p.adjust.method.G = "none", p.adjust.method.D = "none")
##
## ---
##
##                  Test Stat          Obs     Std.Obs     Alter Pvalue
## 1  AxcR1 / very.small    r  0.349866838  1.71654586 two-sided 0.0494 *
## 2  AxcR2 / very.small    r -0.181180303 -0.40917924 two-sided 0.7833
## 3       AxcR1 / small    r -0.080221550 -0.11233842 two-sided 0.9031
## 4       AxcR2 / small    r  0.181132292  0.88966876 two-sided 0.4862
## 5      AxcR1 / medium    r -0.326982545 -1.05785695 two-sided 0.3744
## 6      AxcR2 / medium    r  0.113007898  0.63026305 two-sided 0.6358
## 7         AxcR1 / big    r -0.256351785 -0.66393098 two-sided 0.8644
## 8         AxcR2 / big    r -0.005829747  0.40630661 two-sided      1
```

```
## 9    AxcR1 / very.big    r -0.327472843 -0.99388132 two-sided 0.4312
## 10   AxcR2 / very.big    r -0.018147062  0.24051780 two-sided 0.9057
## 11    AxcR1 / deposit    r  0.318728916  1.25419719 two-sided 0.2316
## 12    AxcR2 / deposit    r -0.075808267 -0.26968375 two-sided 0.8494
## 13       AxcR1 / carn    r -0.424821795 -1.43699649 two-sided 0.1792
## 14       AxcR2 / carn    r -0.047411951 -0.01859715 two-sided 0.9821
## 15       AxcR1 / herb    r -0.363215976 -1.11961768 two-sided 0.4083
## 16       AxcR2 / herb    r -0.144538293 -0.28228324 two-sided 0.7652
## 17     AxcR1 / filter    r  0.206098225  1.06126655 two-sided 0.4499
## 18     AxcR2 / filter    r  0.199367556  1.03500404 two-sided 0.4764
##
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

## And RLQ axes and environmental variables
test.rlq.R <- fourthcorner.rlq(RLQ, modeltype=6,  typetest="R.axes", nrepet=9999,
p.adjust.method.G="none", p.adjust.method.D="none")
test.rlq.R

## Fourth-corner Statistics
## ------------------------
## Permutation method  Comb. 2 and 4  (9999  permutations)
##
## Adjustment method for multiple comparisons:   none
## call:  fourthcorner.rlq(xtest = RLQ, nrepet = 9999, modeltype = 6, typetest =
"R.axes",      p.adjust.method.G = "none", p.adjust.method.D = "none")
##
## ---
##
##                      Test   Stat         Obs     Std.Obs     Alter Pvalue
## 1 organic.matter / AxcQ1      r 0.555116301  1.91707587 two-sided 0.0055
## 2       salinity / AxcQ1      r 0.067157399  0.54691290 two-sided 0.6056
## 3       dredg.NO / AxcQ1 Homog. 0.772601224  4.27147757      less      1
## 4      dredg.YES / AxcQ1 Homog. 0.140244349 -1.34738809      less 0.1156
## 5 organic.matter / AxcQ2      r 0.091802745  0.41187374 two-sided 0.7432
## 6       salinity / AxcQ2      r 0.006910982  0.07114331 two-sided 0.9476
## 7       dredg.NO / AxcQ2 Homog. 0.554160998  0.50883949      less 0.6821
## 8      dredg.YES / AxcQ2 Homog. 0.415495576  0.68963944      less 0.7205
##
## 1 **
## 2
## 3
## 4
## 5
## 6
## 7
## 8
##
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

par(mfrow=c(1,2))
plot(test.rlq.Q, type="table", stat="D2")
plot(test.rlq.R, type="table", stat="D2")
```

```
################################################################################
######################
## References
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CAPÍTULO 2

HOW THE FUNCTIONAL DIVERSITY OF POLYCHAETE ASSEMBLAGES IS AFFECTED BY SEDIMENT PARAMETERS IN SUBTROPICAL ESTUARINE SYSTEMS?[2]

[2] Manuscrito a ser submetido para publicação na revista *Estuarine, Coastal and Shelf Science*.

A B S T R A C T

Assessing the functional diversity of benthic invertebrates in aquatic systems that shows high environmental variability, such as estuaries, is relevant to elucidate community patterns and predict processes that operate in the benthic zone. We investigated the functional diversity of benthic assemblages in estuarine systems along the southern and southeastern Brazilian coast, using polychaetes as proxies of the overall benthic associations. We used functional dispersion (FDis) to measure functional diversity and evaluated how FDis is influenced by organic content and granulometric parameters of the sediment through beta regression models. We applied CWM-RDA to assess the importance of these sedimentological parameters on functional traits composition. Polychaete functional diversity was considerably low and correlated positively with total nitrogen and negatively with average grain size. On the other hand, functional trait composition was influenced mainly by organic content (e.g. total nitrogen, total phosphorus, total carbon, and organic matter). These results suggest that functional structure of polychaete assemblages in the studied estuaries is closely linked to ecological processes that occur in the sediment in dependence on organic compounds, which in turn are made available by organisms presenting specific traits.

Keywords: Trait-based approach; Polychaetes; Morphological traits; Sediment parameters; Beta regression models; CWM-RDA.

1. Introduction

Estuaries are semi-closed heterogeneous systems that exhibit a variety of habitats and marked environmental drivers characterized by high spatial variability and typical sediment-fauna dynamics (Perillo et al., 2009; Bernardino et al., 2016; van der Linden et al., 2017). They are transition zones with complex ecological structures and processes, which provide a variety of ecosystem goods and services (Elliott and Whitfield, 2011; Barros et al., 2012). In these changing environments, both local, such as sediment type, and regional drivers (e.g., temperature and salinity) influence biodiversity (Alves et al., 2006). Estuarine species are extremely adapted to environmental fluctuations and respond to them at varying temporal and spatial scales. As a result, estuaries generally present low diverse communities, since only a few species are able to cope with the high environmental variability (Day et al., 2012; Dolbeth et al., 2015; Nebra et al., 2016).

Besides sharing similar background forcings, estuarine systems worldwide support high population densities of benthic species. However, the combined effects of natural and anthropogenic changes may further alter diversity and abundance patterns of estuarine communities (Bremmer, 2008; Elliott and Whitfield, 2011). These effects may, for example, provide even lower richness in estuaries without a necessary loss of ecosystem functions, because estuarine species generally play similar ecological roles – which also means that they share a large number of functional traits with each other (Magalhães and Barros, 2011; Gerisch et al., 2012). Thus, trait-based approaches can make estuarine ecology more predictive, evidencing patterns in the studied ecosystems that are not evident by using only taxonomic criteria (McGill et al., 2006; Webb et al., 2010; Boersma et al., 2016).

Functional diversity (FD) is a biodiversity measure based on the extent, dispersion and relative abundance of species functional traits (e.g., morphological, behavioral, and

physiological features) that can affect or condition ecosystem functioning (Mason et al., 2005; Violle et al., 2007; Luck et al., 2013). Many methods are currently used to quantify functional diversity using the species functional traits. These methods applied to benthic invertebrates can elucidate community patterns as well as predict processes that operate at the benthic compartment (Bremner et al., 2006). The functional diversity approaches can also support conservation actions through the identification of so-called "functional diversity hotspots" (Stuart-Smith et al., 2013, 2015). However, this type of research is still scarce in marine benthic ecosystems of tropical regions, where few estuaries remain close to their pristine state (Barros et al., 2012; Gusmao et al., 2016; Silva-Júnior et al., 2017). Therefore, there is a clear need to intensify the studies aimed to assess benthic functional diversity in coastal environments, especially in tropical estuarine systems.

Since the strength of regional environmental drivers (e.g., the salinity gradient) on estuarine communities is widely recognized, we focus here on understanding how local sediment parameters (organic content and granulometric) can influence benthic diversity, expressed by functional diversity, in subtropical estuarine systems. We used polychaetes as a proxy because they are dominant in estuarine macrobenthic diversity, exhibit a broad range of traits and perform a relevant role in estuarine functioning (Magalhães and Barros, 2011; Otegui et al., 2016; van der Linden et al., 2017). Polychaetes are fundamental for maintaining aquatic ecosystems, as they play an important role in organic matter cycling, turbidity control, and sediment stability through bioturbation (Defeo et al., 2009; Kuhnert et al., 2010). Considering that the structure of benthic communities is highly related to sediment characteristics (Gray, 1974; Coblent et al., 2015), we expect that variation in sediment parameters will lead to correspondingly variation in the functional structure of polychaete assemblages. The aims of this study were (1) to estimate the functional diversity of polychaete assemblages and evaluate their relationship with organic content and granulometric parameters in subtropical estuarine systems

of southern and southeastern Brazil; and (2) to assess how sediment parameters affect functional trait composition.

2. Materials and methods

2.1. Study area and data collection

The study was carried out in four estuarine systems located along the south-southeastern coast of Brazil: Babitonga (Santa Catarina), Guaratuba (Paraná), Laranjeiras (Paraná), and Trapandé (São Paulo) (Table 1; Fig. 1). The bays are part of the region known as the São Paulo Embayment, which extends from the city of Cabo Frio (RJ) to the Santa Marta Cape (Laguna/SC), between 22ºS and 29ºS approximately. The climate of the region is humid subtropical mesothermic, with hot and wet summers. The estuaries occupy the same coastal region and therefore share the processes of formation of the coastal plain, besides being bordered by mangrove swamps (Angulo and Lessa, 1997; Angulo and Souza, 2004) and to be controlled by similar regional environmental drivers (e.g., tidal regime, input of run-off discharges, wave action, geomorphological features, and human activities). Tidal currents and freshwater discharge regulate stratification and mixing processes inside the estuaries, causing seasonal variations on the vertical salinity distribution (Lana et al., 2018).

Information related to biotic and abiotic sampling are detailed in Pieper (2010), who kindly provided the data to this study. In the summer of 2007 (from February to March), nine transects were sampled from the mouth to the interior of each estuary. Four points were established at each transect, and at each point two sediment samples were taken for biological analysis and one for chemical and granulometric analysis of the sediment with a 0.065 m^2 van Veen grab. Biological samples were washed in the field through a 0.5 mm mesh, and the

retained fauna were fixed in neutral formalin (buffered using 4% borax) for later identification. In the laboratory, the samples were again sieved through 1 mm and 0,5 mm meshes, and the macrofauna specimens were preserved in 70% alcohol containing Rose Bengal stain. Then, the samples were sorted under a stereomicroscope and the polychaetes were separated and identified to the lowest possible taxonomic level, using specialized literature and the help of specialists. The validity of taxonomic status was checked and updated from the World Register of Marine Species (WoRMS; http://www.marinespecies.org/).

Sediment parameters (Table A.2) were analyzed from additional grabs taken at each site at the laboratories of Marine Biogeochemistry and Marine Geology at the Center for Marine Studies/Federal Universiy of Paraná. The oxidation methodology described by Strickland and Parsons (1960) was used to analyze total carbon, and the persulfate oxidation technique combined with colorimetric measurement (Grasshoff et al., 1983) were employed to evaluate total nitrogen and total phosphorus. The organic matter content was obtained by gravimetric determination, through incineration in muffle at 550 ^{o}C for one hour.

Table 1. General characteristics of the four systems located in Santa Catarina, Paraná and São Paulo states, south-southeast coast of Brazil.

Estuary	**Latitude**	**Longitude**	**Area (~km^2)**	**Length (~km)**	**Maximum width (~km)**	**Mean depth (m)**
Babitonga	26º16'S	48°41'W	160	27	5	6
Guaratuba	25º52'S	48°38'W	50	15	5	3
Laranjeiras	25º28'S	48º22'W	200	30	11	2.5
Trapandé	25º01'S	47º55'W	135	75	1.6	10

2.2. Data analyses

2.2.1. Functional diversity

As our intention was to identify general patterns of polychaetes functional diversity in subtropical estuarine systems, we treated the estuaries as replicates to compute functional diversity and other statistical analyses. To evaluate the functional diversity of polychaete assemblages at each site of the estuarine systems, we measured the functional dipersion (FDis) index (Laliberté and Legendre, 2010). Functional dispersion estimates variations in the functional traits of the species by calculating the average distance of each species to the centroid of all species in a multivariate trait-space. Thus, high mean values of FDis means high variation in the trait values, indicating a high functional diversity across species of the analyzed environment (Wouters et al., 2018). FDis is independent of the convex hull volume, which makes it less sensitive to outliers compared to functional diversity indices based on this concept, such as measures proposed by Villéger et al. (2008), according to Laliberté and Legendre (2010). In addition, FDis can be calculated from presence/absence data.

For the functional categorization needed to calculate FDis, we selected traits used in previous studies of polychaetes (e.g., Otegui et al., 2016; Wouters et al., 2018). We used a modified classification of Otegui et al. (2016), which allows for standardization of existing trait data into unique morphological characteristics. We used a combination of nine categorical morphological traits composed by 25 categories (Table 2) based on information from Faulwetter et al. (2014), Jumars et al. (2015), Otegui et al. (2016), and personal advice from experts on polychaetes. Data were compiled in a matrix listing only the main category occupied by the taxon for a certain trait. Functional classification was performed at family level, which is not a significant bias, because polychaete families display a broad plasticity in their functional traits,

especially in the morphological characteristics (Martin and Bastida, 2006; Aguado-Giménez et al. 2015). Besides, the approach of functional categorization proposed by Otegui et al. (2016) was conducted for this taxonomic level.

The relationships between FDis and sediment parameters were analyzed using beta regression models, which are commonly used to model variables that assume values in the open standard unit interval (i.e., values between 0 and 1), such as FDis. This approach is based on the assumption that the dependent variable has a beta distribution and that its mean is linked to some regressors through a linear predictor with unknown coefficients and a link function (Cribari-Neto and Zeileis, 2010). We selected the link function "log-log", since it improved the pseudo R^2 of the models. The vif function was used to evaluate the collinearity among the 13 available parameters (Table A.2); 3 variables (sand, silt and fine sediment) were excluded from the analysis because of the presence of collinearity (i.e., vif > 5; Hair et al. 1995). The best model was chosen according to Akaike information criterion (AIC; Burnham and Anderson, 2002).

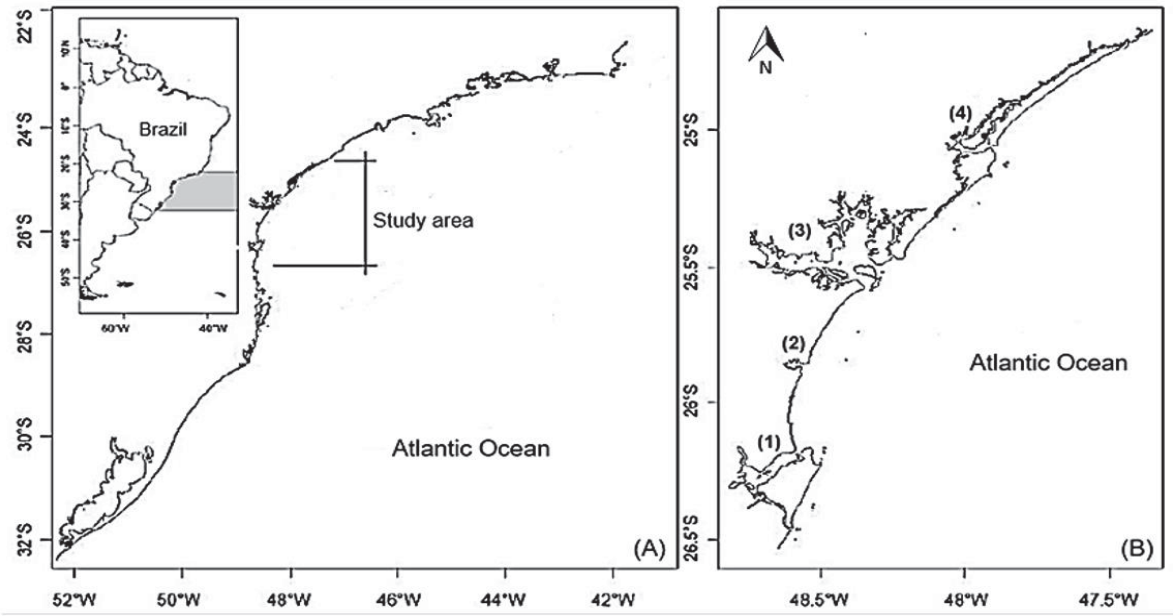

Fig. 1. South-southeastern coast of Brazil (A) and study area (B) with the four studied estuarine systems: (1) Babitonga Bay, (2) Guaratuba Bay, (3) Laranjeiras Bay, and (4) Trapandé Bay.

Table 2. Morphological traits of polychaetes according to Faulwetter et al. (2014), Jumars et al. (2015), Otegui et al. (2016), and ad hoc information from specialists.

Morphological trait	Category	Labels
Pharynx complexity	Absent	PH.ab
	Ventral	PH.ve
	Axial muscular	PH.am
	Axial non-muscular	PH.nm
Jaws presence	Absent	JA.ab
	Present	JA.pr
Feeding structures	Absent	FS.ab
	A pair of structures	FS.ps
	Multiple structures	FS.ms
Sensory appendages	Absent	SA.ab
	Only one structure	SA.os
	Multiple structures	SA.ms
Body appendages	Absent	BA.ab
	Present	BA.pr
Chaetal (parapodia) pattern	Parapodia uniramous simple	CP.us
	Parapodia uniramous with uncini or hook	CP.uh
	Parapodia biramous simple	CP.bs
	Parapodia biramous with uncini or hook	CP.bh
Branchiae regionalization	Absent	BR.ab
	Regionalized	BR.re
	Non-regionalized	BR.nr
Body regionalization	Regionalized	BO.re
	Non-regionalized	BO.nr
Number of segments	≤ 100	SE.100
	≥ 101	SE.200

2.2.2. Functional composition: CWM-RDA

To assess the influence of sediment parameters on functional trait composition, we applied a community-weighted mean redundancy analysis (hereafter referred to as CWM-RDA). This procedure is useful to reveal patterns in average trait expressions regarding environmental variables (Kleyer et al., 2012). First, from sites-by-taxa and taxa-by-traits matrices, a site-by-traits matrix was constructed to represent the trait composition at the community level. This new

matrix is a CWM matrix (i.e., community-weighted mean trait values; Garnier et al., 2007) that defines the dominant traits in a community. As we are dealing here with presence/absence data, the CWMs were calculated through the average of trait values weighted by the relative frequencies of taxa in each sampling site. We then performed the RDA using the CWM matrix constrained by the matrix with the values of sediment parameters. We again excluded the parameters sand, silt and fine sediment from the analysis due to the presence of collinearity. Finally, the significance provided by the CWM-RDA was evaluated by a permutation test. All analyses were performed using the software R (R Core Team 2017) and the packages *FD* (Laliberté et al., 2014), *faraway* (Faraway, 2016), *betareg* (Cribari-Neto and Zeileis, 2010), and *vegan* (Oksanen et al., 2011).

3. Results

We identified and functionally categorized 37 polychaete taxa in the four subtropical estuarine systems (Table A.1). In relation to the nine functional traits, the categories PH.ve (15 taxa), JA.ab (24 taxa), FS.ps (21 taxa), SA.ms (15 taxa), BA.pr (23 taxa), CP.bs (18 taxa), BR.nr (12 taxa), BO.nr (25 taxa), and SE.200 (19 taxa) were the most abundant. We observed low values of functional diversity in polychaete assemblages of the four studied estuarine systems (Table A.2). These values were highly affected both by organic content and granulometric parameters of the sediment. The best beta regression model retained total nitrogen and average grain size as best predictors for variation in FDis (pseudo R^2= 0.1053; Table 3). The model showed a significant positive relation of FDis with nitrogen ($p< 0.05$; Fig. 2a), and a significant negative relation wih average grain size ($p< 0.001$; Fig. 2b).

Table 3. Results of the beta regression models of the relationship between functional dispersion and sediment parameters. (a) Akaike Information Criterion (AIC) of the five best models. (b) Parameter estimates of the best model. (matter= organic matter; grain= average grain size).

a

Sediment parameters	df	AIC
nitrogen x grain	4	-357.7
carbon x grain	4	-357.5
grain x clay	5	-357.3
nitrogen x carbon x matter x grain	6	-357.2
carbon x matter x grain	5	-357.1

b

	Estimate	SE	p-value
Intercept	0.13847	0.044189	0.001727
Nitrogen	0.004204	0.002093	0.044535
Grain	-0.042537	0.011605	0.000247

The two axes of CWM-RDA retained for interpretation explained 71.3% of the total variance, gathering the most important correlations between sediment parameters and functional trait composition. The percentage of explanation provided by the analysis was significant according to the permutation test ($p< 0.05$). The results indicated a higher influence of organic parameters in explaining the significant morphological traits of polychaete assemblages along the southern and southeastern Brazilian coast. In the positive part of CWM-RDA axis 1, the analysis showed a strong association between total nitrogen, total phosphorus, total carbon and degree of sediment selection, and polychaete taxa with ventral pharynx (PH.ve), without sensory (SA.ab) and body appendages (BA.ab), and with parapodia biramous with uncini or hook (CP.bh). On the other hand, organic matter was mostly related to polychaetes with axial non-muscular pharynx (PH.nm), without jaw (JA.ab), and number of segments ≤ 100 (SE.100) in the positive parte of axis 2; and polychaetes with jaw (JA.pr) and number of segments ≥ 101 (SE.200) were associated with gravel in the negative part of the same axis (Fig. 3).

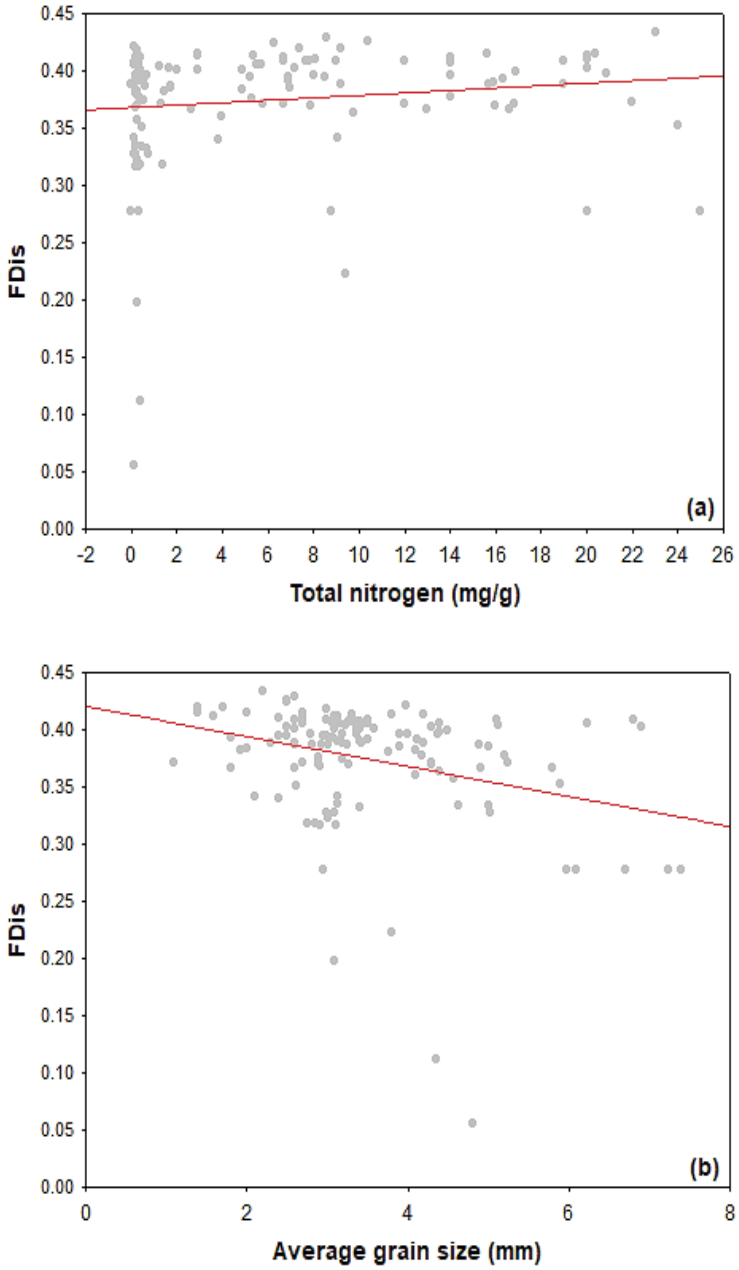

Fig. 2. Relationships between polychaete functional diversity (FDis) and the sediment parameters (a) total nitrogen and (b) average grain size, as considered in the best beta regression model.

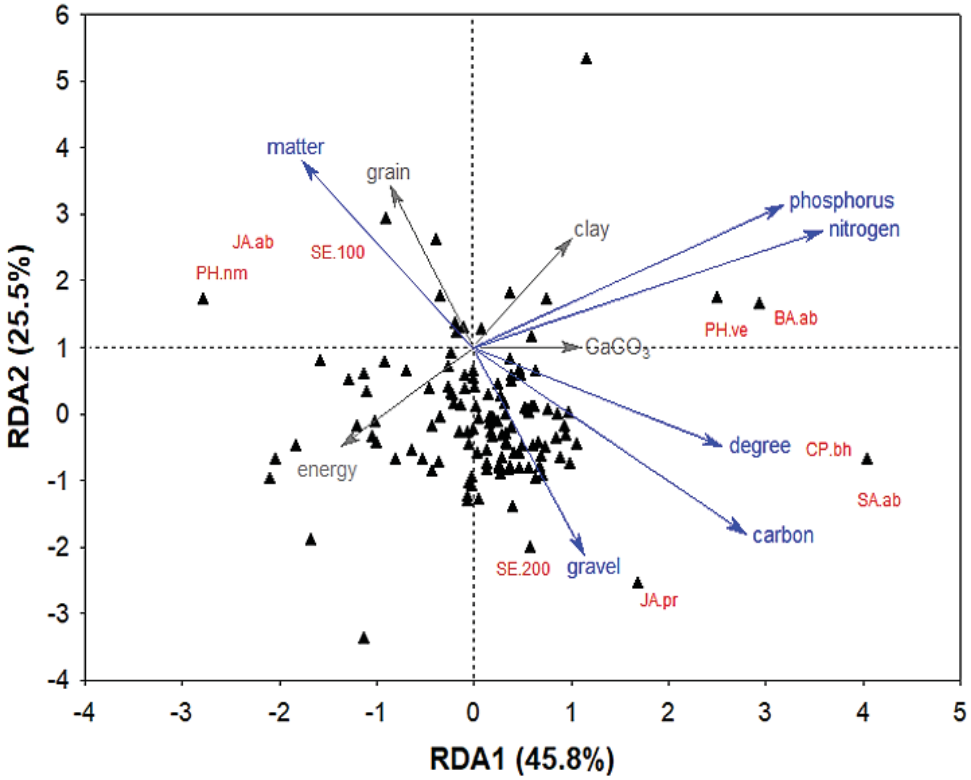

Fig. 3. Ordination diagram for the first two axes of CWM-RDA. Blue arrows illustrate strong influence of the sediment parameter on the significant traits of polychaetes assemblages in estuarine systems, while gray arrows indicate weak influence (matter= organic matter; grain= average grain size; degree= degree of sediment selection; energy= hydrodynamic energy). See Table 2 for the corresponding trait modalities labels.

4. Discussion

Environmental drivers strongly affect estuarine macrobenthic communities and may be responsible for low taxonomic and functional diversity (Elliott and Quintino, 2007; Nebra et al., 2016). Our results indicated that the polychaete functional diversity in subtropical estuarine systems of southern and southeastern Brazil was low and mainly influenced by two parameters, total nitrogen and average grain size. The analyzed parameters – mainly the organic ones (e.g., total nitrogen, total phosphorus, total carbon and organic matter) – also strongly influenced the

functional trait composition of polychaetes, as illustrated by the CWM-RDA. Thus, as expected, variation in sediment parameters markedly affected the functional structure of polychaete assemblages, and this was expressed mainly on the functional composition.

Low levels of functional diversity were previously reported in estuaries (e.g., Dolbeth et al., 2016, Silva-Júnior et al., 2017, van der Linden et al. 2017). Due to marked abiotic fluctuations occurring in these environments, estuarine communities are generally characterized by few and highly adapted dominant species, which perform similar ecological functions (Day et al., 2012; van der Linden et al., 2016). The ability of species to cope with high environmental variability is expectedly followed by a low functional diversity and a high functional redundancy (i.e., many species playing similar roles), as a large number of trait modalities are shared by most dominant taxa (Magalhães and Barros, 2011; Darr et al., 2014). Consequently, estuaries seem to be less vulnerable to declines in ecosystem functioning by the loss of a single or a few species. Such attribute is relevant to assess the consequences of natural and anthropogenic changes, since vulnerable communities are less resistant and less resilient to disturbances (Guillemot et al. 2011).

It is well known that the benthic structure and function are dependent of both sediment and water characteristics in aquatic ecosystems (Elliott and Whitfield, 2011). The combination of such factors shapes estuarine gradients that causes responses in faunal diversity. According to the best beta regression model, we found that most of the variation in functional diversity (expressed by FDis) is explained by total nitrogen and average grain size. The selection of only two among the 10 parameters available suggests that FDis may also respond to other abiotic variables not included in our models. The salinity variation, for example, has been identified as the main driver of macrofaunal distribution and diversity in estuaries (Nebra et al., 2016), but was not evaluated in this study.

Contents of sand, silt and fine sediment (Table A.2) were considered multicollinear and withdrawn from data analyzes. The use of many explanatory variables inevitably increases the multicollinearity, generating unstable or unreliable inferences (Nally, 2002; Dormann et al., 2013). Anyway, this is a statistical problem often implicit in regression methods, such as beta regression and CWA-RDA. In other words, the highly correlated variables should be removed from the model because they inflate the standard error and cause large changes in the coefficient estimates, making the extrapolation of the results beyond the study area inappropriate (Graham, 2003). Estuarine sediments are relatively heterogeneous and, as confirmed by our observations, the components sand, silt and fine sediment contribute in high proportions to the spatial heterogeneity (Green et al., 1997, 2000). In the present study, we can consider that the relative importance of the three parameters is being represented by average grain size that was selected in the best beta regression model.

Grain size is the most basic physical property of sedimentary systems. Fine-grained sediments assume primary importance in estuaries, since they are easily transported along entire systems through the movement of water caused by winds, rivers, tides and waves (Hossain et al., 2014). We found that higher values of functional diversity were related to smaller grain sizes. Similar trends were described for macrobenthic diversity (Rodil et al., 2014) and also for polychaete taxonomic (Defeo and McLachlan, 2011) and functional diversity (Wouters et al., 2018). The spatial complexity in the studied estuaries is due to geomorphological and hydrodynamic features that lead a corresponding heterogeneity of the benthic habitats and associated assemblages (Lana et al., 2018). The decrease in grain size can contribute to habitat complexity in specific sectors of the estuaries (e.g., towards the internal sector), providing higher taxonomic and functional diversities. Besides, the importance of biogeochemical changes modulated by bioturbation in sediments increases as grain size decreases (Mermillod-Blondin, 2011). The activity of bioturbation by the polychaetes, in turn, is closely dependent to their

morphological and life history traits (Faulwetter et al., 2014). This would also explain an increase in functional traits diversity in habitats with smaller grain sizes.

The influence of organic content on functional diversity and functional composition of polychaete assemblages were evidenced in the four subtropical estuaries. We observed that high values of total nitrogen were always related to high functional diversity. On the other hand, all the organic variables analyzed were important for predicting the functional characteristics of the assemblages. Estuaries are considered highly productive environments since they present high levels of nutrients and organic matter (Costanza et al., 1997; Silva-Júnior et al., 2017). In tropical and subtropical estuaries this is especially true because mangroves contribute actively to the increase of organic matter, being also important to carbon production/consumption and nutrient cycling that occurs typically near the substrate (Rezende et al., 2007), where the macrobenthic community play a major role in this regard. In addition to bioturbation, which is crucial to aerate and remobilize the sediment, polychaetes actively participate in the breakdown, subduction, and integration of nutrients and organic matter into sediments (Rengaiyan et al., 2017). All these activities support relevant ecological processes, such as nutrient cycling, secondary production, and energy flows. In subtropical estuarine systems of southern and southeastern Brazil, polychaete taxa without jaws, with ventral or axial non-muscular pharynx, without sensory and body appendages, with parapodia biramous with uncini or hook, and number of segments ≤ 100 seem to be fundamental on the availability of organic compounds for processes that depend on these in the sediment, as evidenced by CWM-RDA results.

This combination of traits is shared between dominant taxa, which ultimately decreases functional diversity and increases functional redundancy in estuaries. This scenario may become still more evident since estuaries and estuarine resources are subject to increasing human usage. Major man-made disturbance, such as construction and dredging of canals, effluent discharge, excessive input of organic matter and nutrients that cause eutrophication (N and P), solid waste

pollution, and introduction of exotic species (Mann, 2000), drastically alter the abiotic variables and consequently change species composition, benefiting the dominance of tolerant taxa. These taxa can share an even larger number of traits among themselves, favoring some ecological functions to the detriment of others. The studied estuaries are located in a region under high disturbance levels by human activities (Lana et al., 2018), which could favor this type of situation. Therefore, the conservation of estuarine systems along the southern and southeastern Brazilian coast will be essential to maintain the diversity and functions in an area with a variety of anthropogenic disturbances.

In summary, our study adds evidence on the importance of organic content and granulometric parameters of the sediment in the functional structure of polychaete assemblages in subtropical estuarine systems. It also highlights the relation of these parameters with functional trait composition, revealing some aspects of functional organization. Our findings support the premise that the biodiversity of estuarine benthic communities is affected by the synergism of water and sediment properties, which are regulated by the natural and human-induced stress imposed on these environments. However, as in most investigations, our results have limitations. Although polychaete families shows high morphological plasticity, the functional classification at the family level can lead to a certain loss of information. Besides, changes in functional diversity can be affected by abundance (Mason et al., 2005), and here we used only presence/absence data. In any case, we provided consistent and relevant information about benthic functional diversity in environments still poorly explored, as is the case of subtropical estuaries. Future research should focus on testing the generality of conclusions, as well as on providing new insights about environmental drivers of macrobenthic estuarine function.

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Table A.1. Morphological traits of polychaetes sampled in four subtropical estuarine systems of southern and southeastern Brazilian coast (PH.ab= absent; PH.ve= ventral; PH.am= axial muscular; PH.nm= axial non-muscular; JA.ab= absent; JA.pr= present; FS.ab= absent; FS.ss= a single structure; FS.ps= a pair of structures; FS.ms= multiple structures; SA.ab= absent; SA.os= only one structure; SA.ms= multiple structures; BA.ab= absent; BA.pr= present; CP.ab= all parapodial features absent; CP.us= parapodia uniramous simple; CP.uh= parapodia uniramous with uncini or hook; CP.bs= parapodia biramous simple; CP.bh= parapodia biramous with uncini or hook; BR.ab= absent; BR.re= regionalized; BR.nr= non-regionalized; BO.re= regionalized; BO.nr= non-regionalized; SE.100= ≤ 100 segments; SE.200= ≥ 101segments).

Family	Morphological trait								
	Pharynx complexity	**Jaws presence**	**Feeding structures**	**Sensory appendages**	**Body appendages**	**Chaetal (parapodia) pattern**	**Branchiae regionalization**	**Body regionalization**	**Body size**
Ampharetidae	PH.ve	JA.ab	FS.ms	SA.ab	BA.ab	CP.bh	BR.re	BO.re	SE.100
Amphinomidae	PH.ve	JA.ab	FS.ps	SA.ms	BA.pr	CP.bs	BR.nr	BO.nr	SE.200
Capitellidae	PH.nm	JA.ab	FS.ab	SA.ab	BA.ab	CP.uh	BR.ab	BO.nr	SE.100
Chaetopteridae	PH.ve	JA.ab	FS.ps	SA.ab	BA.ab	CP.bs	BR.ab	BO.re	SE.100
Cirratulidae	PH.ve	JA.ab	FS.ps	SA.os	BA.ab	CP.bh	BR.nr	BO.nr	SE.200
Dorvilleidae	PH.ve	JA.pr	FS.ps	SA.ms	BA.ab	CP.bs	BR.nr	BO.re	SE.200
Eunicidae	PH.ve	JA.pr	FS.ps	SA.ms	BA.pr	CP.bs	BR.nr	BO.nr	SE.200
Fabriciidae	PH.ab	JA.ab	FS.ms	SA.os	BA.ab	CP.uh	BR.re	BO.re	SE.100
Flabelligeridae	PH.ve	JA.ab	FS.ps	SA.os	BA.ab	CP.bs	BR.re	BO.nr	SE.100
Glyceridae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.bs	BR.ab	BO.nr	SE.200
Goniadidae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.bs	BR.ab	BO.nr	SE.200
Hesionidae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.bs	BR.ab	BO.nr	SE.100
Iospilidae	PH.am	JA.pr	FS.ps	SA.os	BA.pr	CP.us	BR.ab	BO.nr	SE.200
Lumbrineridae	PH.ve	JA.pr	FS.ab	SA.ab	BA.pr	CP.bh	BR.ab	BO.nr	SE.200

Magelonidae	PH.ve	JA.ab	FS.ps	SA.ab	BA.ab	CP.bh	BR.ab	BO.re	SE.200
Maldanidae	PH.nm	JA.ab	FS.ab	SA.ab	BA.ab	CP.bs	BR.ab	BO.nr	SE.100
Nephtyidae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.bs	BR.nr	BO.nr	SE.200
Nereididae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.bs	BR.ab	BO.nr	SE.200
Onuphidae	PH.ve	JA.pr	FS.ms	SA.ms	BA.pr	CP.bh	BR.nr	BO.nr	SE.200
Opheliidae	PH.nm	JA.ab	FS.ab	SA.ab	BA.pr	CP.bs	BR.nr	BO.re	SE.100
Orbiniidae	PH.nm	JA.ab	FS.ab	SA.ab	BA.ab	CP.bs	BR.re	BO.nr	SE.100
Oweniidae	PH.ve	JA.ab	FS.ms	SA.os	BA.ab	CP.bh	BR.ab	BO.nr	SE.100
Paraonidae	PH.nm	JA.ab	FS.ab	SA.os	BA.pr	CP.bs	BR.re	BO.nr	SE.200
Pectinariidae	PH.ve	JA.ab	FS.ms	SA.os	BA.pr	CP.bh	BR.re	BO.re	SE.100
Pholoidae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.bs	BR.nr	BO.nr	SE.100
Phyllodocidae	PH.am	JA.ab	FS.ps	SA.ms	BA.pr	CP.us	BR.ab	BO.nr	SE.200
Pilargidae	PH.am	JA.ab	FS.ps	SA.ms	BA.pr	CP.bs	BR.nr	BO.nr	SE.100
Poecilochaetidae	PH.ve	JA.ab	FS.ps	SA.os	BA.ab	CP.bs	BR.nr	BO.re	SE.200
Polynoidae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.us	BR.ab	BO.nr	SE.100
Sabellidae	PH.ab	JA.ab	FS.ms	SA.os	BA.pr	CP.uh	BR.re	BO.re	SE.100
Serpulidae	PH.ab	JA.ab	FS.ms	SA.os	BA.ab	CP.uh	BR.re	BO.re	SE.100
Sigalionidae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.bs	BR.nr	BO.nr	SE.200
Spionidae	PH.nm	JA.ab	FS.ps	SA.os	BA.pr	CP.uh	BR.nr	BO.nr	SE.100
Sternaspidae	PH.nm	JA.ab	FS.ab	SA.ab	BA.ab	CP.uh	BR.re	BO.nr	SE.100
Syllidae	PH.am	JA.ab	FS.ps	SA.ms	BA.pr	CP.us	BR.ab	BO.nr	SE.200
Terebellidae	PH.ve	JA.ab	FS.ms	SA.os	BA.pr	CP.bh	BR.re	BO.re	SE.200
Trichobranchidae	PH.ve	JA.ab	FS.ms	SA.os	BA.pr	CP.bh	BR.re	BO.re	SE.200

Table A.2. Mean values(±SD) of biotic and abiotic data (sediment parameters) of subtropical estuarine systems of southern and southeastern Brazil, displayed also for each estuary individually (Bab = Babitonga, Gua = Guaratuba, Lar = Laranjeiras, Tra = Trapandé).

		Estuaries			
		Bab	**Gua**	**Lar**	**Tra**
Diversity					
Richness	8.00±4.00	8.00±6.00	6.00±2.00	7.00±4.00	7.00±4.00
Functional diversity (FDis)	0.37±0.05	0.37±0.08	0.34±0.09	0.36±0.11	0.35±0.12
Organic parameters					
Total nitrogen (mg/g)	5.86±6.92	12.61±6.35	0.63±0.67	10.97±6.43	0.30±0.14
Total phosphorus (mg/g)	2.54±2.56	5.42±3.54	0.95±0.96	3.19±1.59	1.11±0.74
Total carbon (mg/g)	30.29±12.48	33.55±10.81	22.33±9.15	37.16±10.20	26.63±13.53
Organic matter (%)	4.17±3.26	4.62±3.31	5.20±3.64	2.00±1.15	5.48±3.77
Granulometric parameters					
Average grain size (mm)	3.50±1.24	3.64±1.86	3.68±1.00	3.12±0.83	3.82±1.12
Degree of sediment selection	1.49±0.72	1.95±0.84	1.11±0.63	1.66±0.65	1.36±0.40
Gravel (%)	1.60±5.91	5.20±11.00	0.39±0.96	0.60±1.66	0.19±0.50
Sand (%)	75.21±24.10	59.38±31.85	78.74±22.35	82.93±10.15	74.66±24.46
Silt (%)	15.31±20.29	23.63±25.29	16.45±20.90	7.34±6.58	17.58±23.65
Clay (%)	7.88±8.00	11.80±13.59	4.42±5.82	9.14±5.28	7.56±2.34
Fine sediment (%)	23.19±23.13	35.44±30.86	20.87±22.58	16.47±10.12	25.14±24.49
$CaCO_3$ (%)	5.07±2.50	5.92±3.35	5.24±2.12	3.43±1.62	6.28±1.96
Hydrodynamic energy	11.53±18.35	11.00±20.00	16.62±23.50	10.49±16.92	6.34±4.51

CAPÍTULO 3

INVESTIGATING FUNCTIONAL REDUNDANCY IN POLYCHAETE ASSEMBLAGES OF THE SOUTH BRAZIL SHELF LARGE MARINE ECOSYSTEM (SBSLME)[3]

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ABSTRACT: Innovative investigations are needed to help understanding the conservation facet known as functional redundancy (i.e. different species performing similar functions in an ecosystem), especially in the poorly explored tropical coasts. Here we investigated levels of functional redundancy in polychaete assemblages in the tropical continental shelf and estuarine environments of the South Brazil Shelf Large Marine Ecosystem (SBSLME). To quantitatively evaluate the functional redundancy, we used functional originality (FOri) and functional uniqueness (FUni). We reported 61 and 48 polychaete taxa distributed in 50 and 42 functional entities (i.e. a unique combination of trait values) in continental shelf and estuarine environments, respectively, which suggests a low functional redundancy in both environments. We observed significant differences in FOri and FUni between environments; while originality was higher in the estuarine environment, uniqueness was higher in the continental shelf. These results indicate that although estuarine polychaetes have fewer unique combinations of trait values, these combinations are more original and adequate to the varying conditions imposed by estuarine drivers.

KEY WORDS: Benthic community · Functional diversity · Functional entity · Continental shelf · Estuarine environment · Tropical systems · South Brazil Shelf Large Marine Ecosystem

INTRODUCTION

Polychaetes, a diverse group of marine worms, usually dominate the macrobenthic communities of coastal and continental shelf areas (Rouse & Pleijel 2001, Musco 2012, Dorgham et al. 2014). The biogeography of polychaetes tends to represent the patterns of the whole macrofauna (Hughes et al. 2009). For this reason, polychaete assemblages have been commonly used as surrogates or proxies for the biodiversity of marine benthic communities as a whole. These annelids display a high functional trait plasticity, and putatively a high functional diversity (Martin & Bastida 2006, Otegui et al. 2016, van der Linden et al. 2017) with many supported functions or roles in benthic ecosystems. Polychaetes actively participate in relevant marine ecological processes, such as bioturbation, which contributes to aerate and remobilize the sediment, to nutrient cycling, to secondary production, and to energy flow (Faulwetter et al. 2014, Dolbeth et al. 2015, van der Linden et al. 2017, Wouters et al. 2018).

However, even a large amount of functional diversity can be very vulnerable and led to local extinction if, for instance, each function, expressed by a unique combination of traits, is supported by a few or a single species. On the other hand, each function can be supported by many species, a conservation facet coined as functional redundancy (Fonseca & Ganade 2001, Luck et al. 2013, Ricotta et al. 2016). The functional diversity of polychaete assemblages is well documented (e.g. Otegui et al. 2016, van der Linden et al. 2017, Wouters et al. 2018), but little is known about the level of functional redundancy. Functional redundancy assumes a critical relevance nowadays, considering that benthic communities are under serious threat worldwide, due to the growing degradation of the seafloor resulting from habitat loss, hydrodynamic alteration, pollution, and climate change (Danovaro et al. 2008, Defeo et al. 2009, Bernardino et al. 2016). Functional redundancy is anticipated to be higher in the tropics where many species are likely to share the same traits and play the same role. However, over-redundancy, i.e. the disproportional packing of species richness in some functional groups to the detriment of others,

challenges this view. High species richness may or may not guarantee a concomitant high functional redundancy depending on the evaluated ecosystem or type of communities (Mouillot et al. 2014). Much remains to be discovered about the real level of functional redundancy especially in marine environments within tropical systems, where considerable large-scale changes have occurred without rigorous documentation (Jackson 2001, Feng et al. 2018). Due to the increasing number of ecological studies addressing functional redundancy in the last decades, an array of measures has been proposed to quantify this property (Ricotta et al. 2016). Functional originality (FOri) and functional uniqueness (FUni) are two interesting facets of functional redundancy that have been overlooked, despite the valuable information they can provide. These indices characterize the position of a species in the functional space compared to other species of the pool (Buisson et al. 2013, Mouillot et al. 2013).

In this paper we report levels of functional redundancy in polychaete assemblages of the continental shelf and estuarine environments in the South Brazil Shelf Large Marine Ecosystem (SBSLME). We have used a detailed dataset of taxa occurrences and functional traits to examine (1) the distribution of species across different "functional entities" (i.e. a unique combination of trait values sensu Mouillot et al. 2014) in continental shelf and estuarine environments; and (2) the functional redundancy patterns (expressed by FOri and FUni) in the assemblages of these two environments. Since environmental stressors operating in estuarine systems can provide high convergent evolution (i.e. many different species sharing similar functional traits), we expect that functional redundancy will be lower in continental shelf than in estuarine environments. Considering that both indexes are inversely related to functional redundancy, then the originality and uniqueness values should be lower in estuarine environments.

MATERIALS AND METHODS

Construction of taxonomic composition and functional traits matrices

We extracted the occurrence data from NONATObase (Pagliosa et al. 2014), a database for polychaetes from the southwestern Atlantic Ocean. We considered all the soft-bottom records from continental shelf and estuarine environments of the South Brazil Shelf Large Marine Ecosystem (SBSLME). The SBSLME covers an area of about 565,500 km^2 and has a wide continental shelf, encompassing the Brazilian states of Rio de Janeiro, São Paulo, Paraná, Santa Catarina and Rio Grande do Sul (Ekau & Knoppers 2003). It represents the only coastal sector in Brazil with a subtropical to temperate climate (Mahiques et al. 2010). In total, presence/absence data from 1,234 sites from continental shelf and 347 sites from estuarine environments, ranging from ~22ºS to ~34ºS (i.e. the latitudinal extension of the SBSLME), were used to construct the matrices listing polychaetes occurrences.

We used a functional categorization based on the morphological characteristics of polychaetes, modified from Otegui et al. (2016). This classification allows for a standardization of existing trait data into unique morphological characteristics, which eliminates the main subjectivities of the analytical process (Otegui et al. 2016). We selected a combination of nine categorical morphological traits composed by 27 attributes/categories (Table 1, Table S1). Information for polychaete families were obtained from Faulwetter et al. (2014), Jumars et al. (2015), and Otegui et al. (2016), besides ad-hoc opinion of experts. The family level was previously recognized as capable of showing accurate and robust ecological patterns for polychaetes (Muniz & Pires-Vanin 2005, Aguado-Giménez et al. 2015). We followed a simple classification considering only the primary attribute for each characteristic (i.e. each family holds only one of the categories for the trait considered).

Measuring and analyzing functional redundancy

Following Mouillot et al. (2014), the total number of functional entities (FEs) was defined as unique combinations of the nine morphological traits. FEs were computed for each taxon (family) using the R function "species_to_FE" (described in the Supplement) and the number of FEs was reported for each environment. From this function, some metrics can be extracted for each assemblage, such as functional redundancy (i.e. the mean number of species per FE; Fonseca & Ganade 2001), functional over-redundancy (i.e. the percentage of species in excess in FEs containing more species than expected from functional redundancy; Mouillot et al. 2014), and functional vulnerability (i.e. the percentage of functional entities containing only one species; Bihn et al. 2010). The function also returns the presence data of the taxa in functional entities. In order to visualize similarities in FEs in continental shelf and estuarine environments, we used these data to perform a Principal Coordinates Analysis (PCoA; Laliberté & Legendre 2010) based on Jaccard's distance matrices (Jaccard 1912).

The many facets of functional diversity can be measured within a multidimensional space derived from the set of functional traits which were quantified (Villéger et al. 2008, Mouchet et al. 2010). Following Villéger et al. (2008) and Buisson et al. (2013), we constructed a multidimensional functional space using the 27 categories of functional traits. First, a functional distance matrix was computed for each pair of species using Gower's distance (Gower 1966) that accepts any type of trait data, including categorical and/or ordinal measures. This distance matrix was then employed to carry out a PCoA (Laliberté & Legendre 2010), using the Cailliez correction to accommodate negative eigenvalues. The scores of the first three axes of the PCoA were kept to build the multidimensional functional space, which provides a clear picture of the relationships among species functional traits. All morphological traits were overlaid as vectors to discriminate the sources of the differences among species.

To evaluate functional redundancy patterns in polychaetes assemblages of continental shelf and estuarine environments we used the functional originality (FOri) and functional uniqueness (FUni) indices (Buisson et al. 2013, Mouillot et al. 2013). Functional originality corresponds to the isolation degree of a species at the functional niche, in relation to the average rarity of its functional attributes (Pavoine et al. 2005, Mouillot et al. 2008, 2013). However, this measure does not consider that two species can share a unique combination of traits that is not present in the other species of the pool. Thus, functional uniqueness describes this additional facet of the biological identity of species, representing approximately the opposite of functional redundancy (Buisson et al. 2013, Mori et al. 2016). In practice, high values of FOri means that the investigated species is functionally different from the theoretical average species (i.e. the center of the multidimensional functional space); and high values of FUni indicate that a species has a unique combination of traits compared to each species of the pool (i.e. low redundancy) (Fig. 1; Buisson et al. 2013, Maire et al. 2013). Using the species coordinates in the three-dimensional space defined by the PCoA and species occurrences matrix, the indices were estimated. FOri and FUni of a certain species were defined as the Euclidean distance to the average position of the species and the center of the functional space, and of its nearest neighbor in the species pool, respectively. Since FOri and FUni are not normally distributed, we used the Kruskal-Wallis non-parametrit test (Kruskal & Wallis 1952) to check for significant differences in the values of the indices between continental shelf and estuarine environments.

All the calculations and analyzes were performed using the software R (R Core Team 2017). The procedures and required packages are detailed in the R script available as Supplement material.

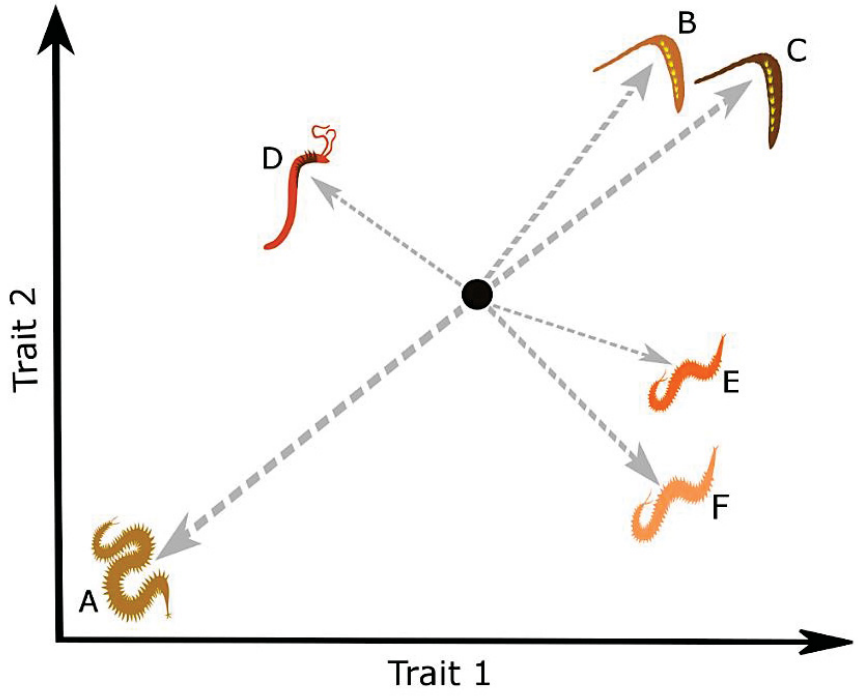

Fig 1. Possible patterns of functional originality and functional uniqueness in a polychaete assemblage. Six species (A-F) of polychaetes are plotted in a two-dimensional functional space. The black circle indicates the center of gravity of this hypothetical species pool. If the species is far from the center it is considered original, if close to the center it is not original. On the other hand, if the species is functionally different from the other species, is unique. However, if close to another species in the functional space, it is functionally redundant. In the figure, species A is functionally original and unique; species B and C are original, but functionally redundant; species D is not original, but is unique; and species E and F are not original and are functionally redundant (adapted from Buisson et al. 2013).

Table 1. Trait classification used in the trait matrix, according to Faulwetter et al. (2014), Jumars et al. (2015), Otegui et al. (2016), and ad hoc information from specialists.

Morphological trait	Category	ID	Description
Pharynx complexity	Absent	PH.ab	Pharynx is an auxiliary buccal organ used for feeding, which also describe on where the organism lives
	Ventral	PH.ve	
	Axial muscular	PH.am	
	Axial non-muscular	PH.nm	
Jaws presence	Absent	JA.ab	Jaws are cuticular structures to resource capture, which also assist in defense and show where the organism lives
	Present	JA.pr	
Feeding structures	Absent	FS.ab	Peristomium appendices that assists in feeding by capturing resources, and also show where the organism lives
	A single structure (palp or tentacle)	FS.ss	
	A pair of structures	FS.ps	
	Multiple structures	FS.ms	
Sensory appendages	Absent	SA.ab	Head structures (e.g. antenna, sensorial palps, and cirrus) used for defense and feeding
	Only one structure	SA.os	
	Multiple structures	SA.ms	
Body appendages	Absent	BA.ab	Lateral organs, statocysts, dorsal organs, and parapodial cirri used for defense and feeding
	Present	BA.pr	
Chaetal (parapodia) pattern	All parapodial features absent	CP.ab	Parapodia are stout un-jointed lateral structures that bear the chaetae, helping in the locomotion and providing support to the body
	Parapodia uniramous simple	CP.us	
	Parapodia uniramous with uncini or hook	CP.uh	
	Parapodia biramous simple	CP.bs	
	Parapodia biramous with uncini or hook	CP.bh	
Branchiae regionalization	Absent	BR.ab	Branchiae are located at the ends or along the body and are responsible for gaseous exchanges that provide energy for the locomotion and feeding
	Regionalized	BR.re	
	Non-regionalized	BR.nr	
Body regionalization	Regionalized	BO.re	The body can be divided in thorax and abdomen or not be divided. Regionalized body provide better mobility
	Non-regionalized	BO.nr	
Body size	≤ 100 segments	SE.100	Body metameres can be little or very segmented. Body size defines life strategies and the ecological niche
	≥ 101segments	SE.200	

RESULTS

To classify the 61 and 48 polychaetes families of the regional pool of continental shelf and estuarine environments (Table A1), we identified respectively 50 and 42 functional entities based on unique combinations of nine categorical morphological traits (Fig. 2, Table S2). This high number of FEs in relation to the number of families – with at most four and three families per FE in continental shelf and estuarine environments, as well as the observed values for FE metrics (Table 2) – indicates a low functional redundancy in both environments.

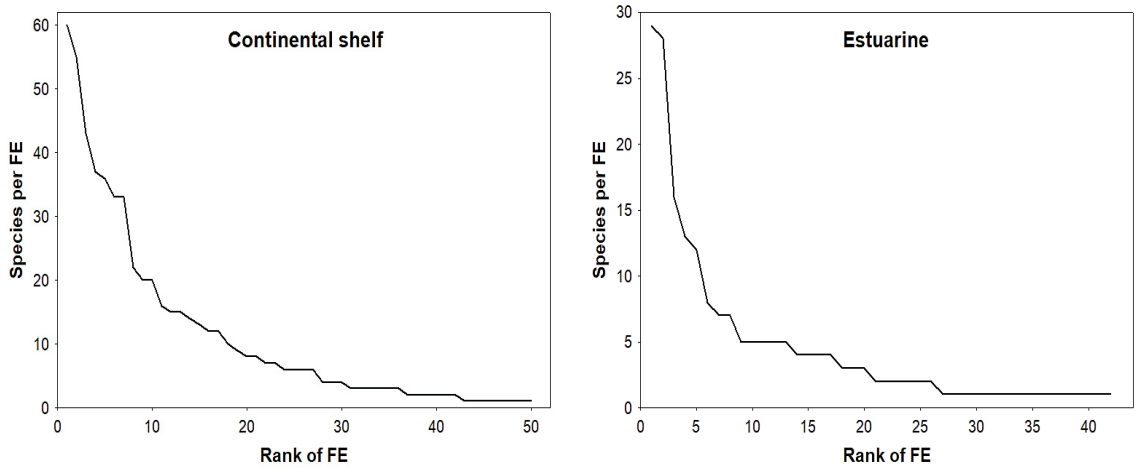

Fig 2. Distribution of polychaete species into functional entities displayed for continental shelf and estuarine environments. For graphical convenience, we counted the total number of species per family, considering all the species of a family belonging to the same FE.

The PCoA ordinations showed differences in functional entities of continental shelf and estuarine environments (Fig. 3). The FEs of continental shelf are separated from each other, which means that the combinations of traits of these FEs are less

similar than the combinations of FEs of the estuarine environments, where FEs are closer to each other.

Table 2. Metrics associated with the functional entities of the polychaetes assemblages of continental shelf and estuarine environments.

FE metrics	Continental shelf	Estuarine
Functional redundancy	1.22	1.14
Functional over-redundancy (%)	15	11
Functional vulnerability (%)	84	88

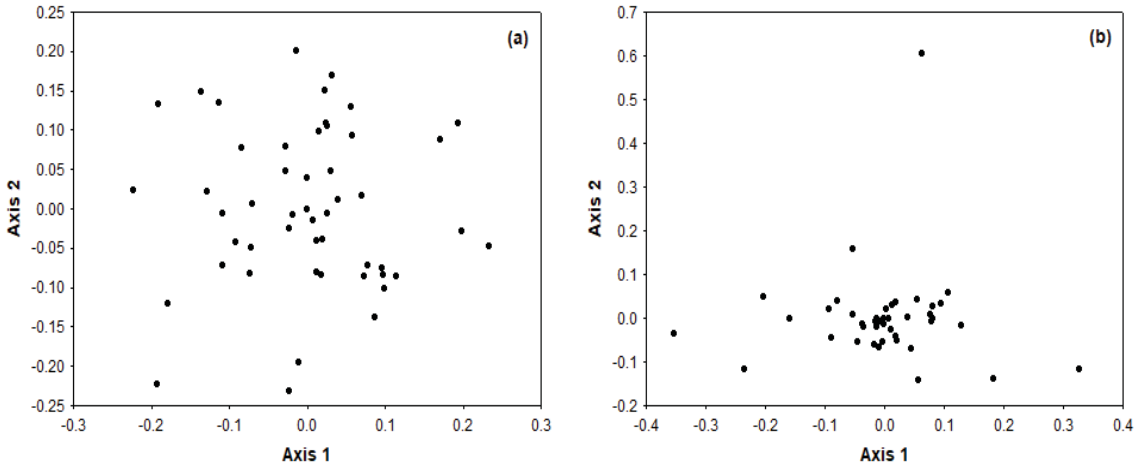

Fig. 3. PCoA ordinations using Jaccard's distance matrices of 50 and 42 functional entities in continental shelf (a) and estuarine environments (b), respectively.

Mean values of originality were higher than the mean values of uniqueness in both environments (Table 3). We observed differences in the functional redundancy patterns assessed by FOri and FUni indices between environments. Functional originality was higher in the polychaete assemblages of estuarine environments (Fig. 4a), whereas functional uniqueness showed higher values in the assemblages of

continental shelf environments (Fig. 4b). The differences between continental shelf and estuarine environments were significant for both indices (Table 3).

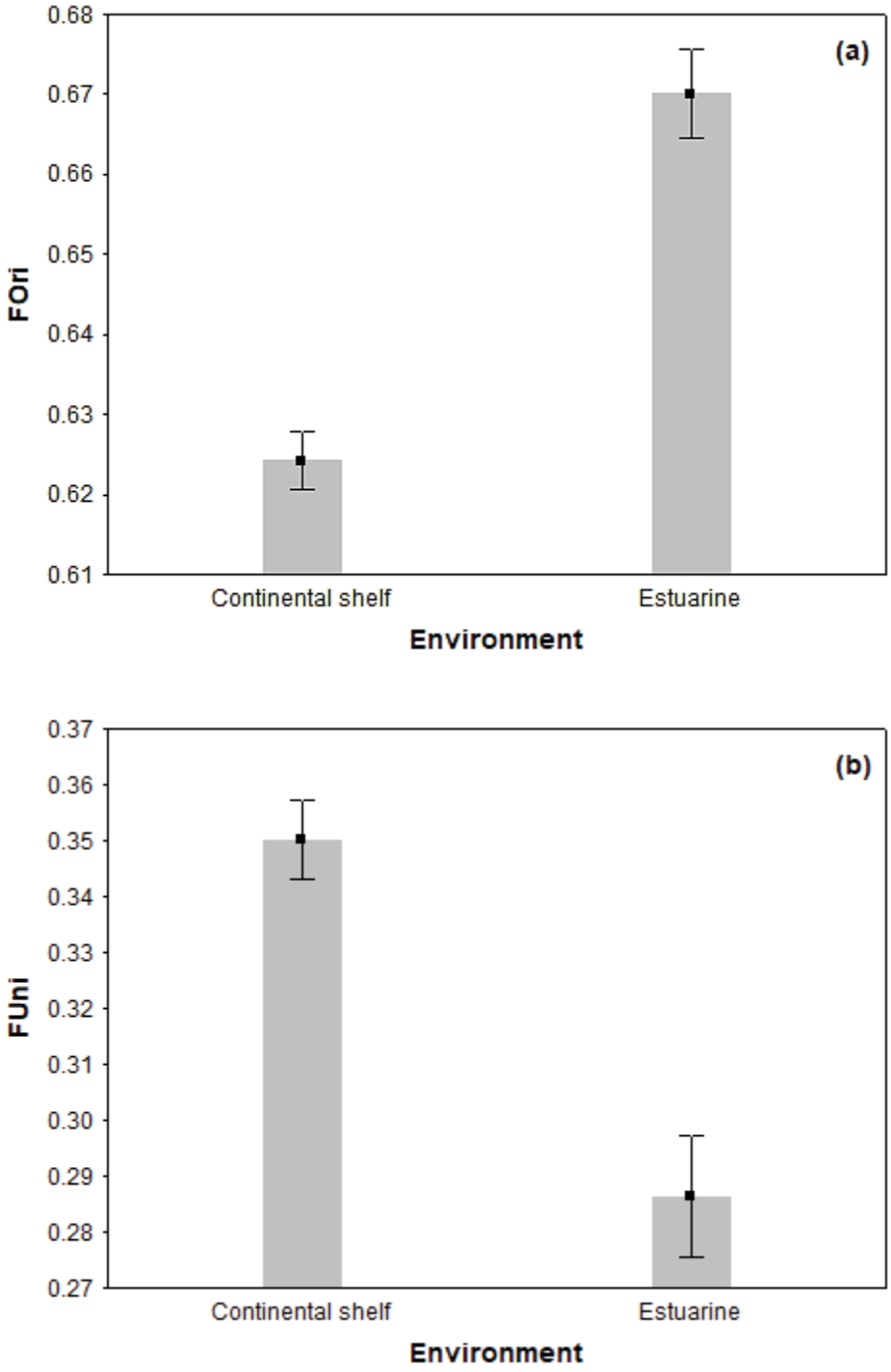

Fig 4. Mean values (SE) of (a) functional originality index (FOri) and (b) functional uniqueness index (FUni) in continental shelf and estuarine environments.

Table 3. Results of Kruskal-Wallis comparing functional originality (FOri) and functional uniqueness (FUni) between continental shelf (n = 1,234) and estuarine (n = 347) environments. Mean values (SE) of each index are reported for each environment.

Index	Continental shelf	Estuarine	*KW-H*	*df*	*P*
FOri	0.624 (0.004)	0.67 (0.006)	71.85	1	< 0.001
FUni	0.35 (0.007)	0.286 (0.011)	25.07	1	< 0.001

DISCUSSION

In general, both estuarine and continental shelf polychaete assemblages along the South Brazil Shelf Large Marine Ecosystem were characterized by low functional redundancy. However, functional redundancy differed significantly between the two environments, as predicted. Higher redundancy (expressed by low functional uniqueness that is roughly the opposite of functional redundancy) was observed in estuarine environments. However, we also found higher values of functional originality in estuarine environments. These results only partially support our working hypothesis, since both indices were expected to exhibit lower values in estuarine environments.

The higher number of functional entities observed in continental shelf environments may result from sampling bias (1,234 sites *vs.* 347 in estuarine environments), which can admittedly lead to an accumulation of information (Zuquim et al. 2007). In other words, the greater sample effort may allow more taxa to be found and thus, more functional entities to be registered. However, considering the number of families observed in each environment, a large number of functional entities were identified in both cases. According to Fonseca & Ganade (2001), communities in which species are distributed in a larger number of functional groups will exhibit less

functional redundancy than communities whose species are distributed in a few functional groups. Following this reasoning, functional entities can be understood under the same context as the functional groups. In total, 50 and 42 FEs were identified based on the classification of 61 and 48 polychaetes families composing the assemblages of continental shelf and estuarine environments, respectively. Most of them (84% and 88%) were supported by only one family, which indicates a low functional redundancy (i.e. if there is only a single taxon for each functional entity, so there is low functional redundancy).

The percentage of FEs with only one taxon is also understood as a measure of the functional vulnerability or, in the ecological sense, of the potential decrease in functional diversity after species loss (Bihn et al. 2010). In ecosystems with low functional redundancy, species loss is usually equivalent to functions loss (Guillemot et al. 2011), and then high environmental vulnerability can be detected, as revealed here by the metrics derived from "species_to_FE" function. Although at lower taxonomic levels (e.g. gender and species) functional redundancy tends to increase since more taxa are identified, the number of unique combinations of traits we reported to polychaete families confirm that functional redundancy was satisfactorily assessed at this taxonomic level. However, we must also consider that we evaluate exclusively morphological aspects of a group presenting high plasticity in these characteristics, which guarantees reliability in the interpretation of results. Communities with considerable morphological variation between families display a greater phylogenetic representativeness and, consequently, an amplification of the occupied functional space (Gatz 1979). Therefore, our findings indicate that polychaete assemblages have low functional redundancy and high vulnerability of ecosystem functions to diversity loss in continental shelf and estuarine environments of the South Brazil Shelf Large Marine Ecosystem.

Low levels of functional redundancy were also reported by Magalhães & Barros (2011) for estuarine assemblages. Although these authors made assumptions about the functional redundancy, they were actually assessing other aspects of the functional structure. More recently, Kokarev et al. (2017) also observed low functional redundancy on macrobenthic communities on a high-Arctic shelf using as a measure the ratio between functional diversity and taxonomic diversity. To our knowledge, our study was the first to investigate the functional redundancy of a benthic assemblage having this as the main research objective, and through metrics closely linked to this purpose. On the other hand, the potential applicability of FUni and FOri has been neglected, since they have only been used together to evaluate fish assemblages in freshwater ecosystems (e.g. Buisson et al. 2013, Maire et al. 2013). Thus, broader comparisons of our findings with other studies is difficult as measures of originality and uniqueness are currently scarce. In addition, both indices are estimated based on species pool so that caution is needed when extrapolating its results outside the study context (Mouillot et al. 2008, Buisson et al. 2013).

In species-rich tropical systems, an increase in functional redundancy is expected, because if one species providing an essential ecosystem function goes extinct, there will probably be another similar species to occupy its place (Fonseca & Ganade 2001, Martins et al. 2012, Mouillot et al. 2014). When many species perform similar functions, functional redundancy ensures that ecosystem functioning continues to operate normally even if there is species loss (Fonseca & Ganade 2001). Recent studies reported high functional redundancy in tropical freshwater assemblages of fish (Casatti et al. 2015) and phytoplankton (Kruk et al. 2017). Conversely, some marine assemblages display little functional redundancy among species in both tropical and temperate ecosystems (e.g. Micheli & Halpern 2005, Guillemot et al. 2011, van der Linden et al.

2012, Magalhães & Barros 2011, Dolbeth et al. 2016, Kokarev et al. 2017). Our results and these previous studies suggest that a low redundancy in the majority of functions may broadly characterize marine assemblages. Thus, besides the specificities of the taxonomic group used as a study tool, the observed patterns can be, at least partially, explained by the historical and evolutionary factors that occur in the marine environments underlying a latitudinal gradient of diversity.

Estuarine systems display characteristics that set them apart from other coastal environments (Fonseca & Netto 2014) and make their biota appropriate for the study of functional aspects. The differences in environmental variables are pronounced in estuaries, and changes in physical, chemical and biological properties result in environmental stress that may be related to low diversity when compared to other marine systems (Alves et al. 2006, Elliott & Whitfield 2011). Environmental stress can provide high convergent evolution (i.e. many different species sharing a large number of functional traits with each other), and so estuarine species generally play similar ecological roles, being also highly specialized to the environment (Magalhães & Barros 2011, Gerisch et al. 2012). The results of PCoAs highlighted this for polychaetes, since the combinations of FEs traits of the estuarine environments were more similar (i.e. with more grouped distribution in the ordination) than the combinations of the FEs traits of the continental shelf.

Similarly, functional uniqueness was used to evaluate the proximity of each polychaete family to its nearest neighbor in the functional space, comparing the unique traits combinations among taxa of the pool (Buisson et al. 2013). Thus, in addition to what was pointed out by the PCoAs ordinations, we observed low values of FUni in estuarine environments (i.e. less functional redundancy). The low values are a consequence of traits mainly shared among the families Nereididae, Capitellidae, and

Spionidae. These families are frequent in regional estuaries, where they possibly perform equivalent estuarine functions. In contrast, polychaete taxa of the continental shelf have a more exclusive combination of traits, and the most frequent families (e.g. Onuphidae, Spionidae, and Lumbrineridae) share few traits among themselves. Unlike estuaries, continental shelf environments are more stable (i.e. they do not undergo extreme variations in the environmental conditions, such as salinity and temperature), and potentially supports a more diverse set of species and consequently, of functional traits.

On the other hand, estuarine polychaete assemblages were more original than continental shelf ones. This means that although estuarine polychaetes are close to each other in the multidimensional functional space, they are far from the center of gravity (i.e. investigated taxa is functionally different from the theoretical average taxon). It has been proposed that the most specialized species are also the most functionally original (Mouillot et al. 2008, Devictor et al. 2010) and, as discussed earlier, estuarine species are fully specialized to the environment. Even if there is high functional redundancy, it is possible to find high functional originality, because the species have an original combination of traits appropriate to a narrow ecological niche within the particular environment in which they live (Buisson et al. 2013, Brandl et al. 2016). Thus, although estuarine polychaetes assemblages have fewer unique combinations of trait values, these combinations are more original and suitable to the varying conditions that are imposed on the environment.

CONCLUSIONS

Polychaete assemblages were generally characterized by low functional redundancy, and significant variation was clearly associated with the type of environment. Higher levels of functional redundancy reported in estuaries indicate that the convergent evolution imposed by environmental stressors play a primary role in the functional structuring of polychaete assemblages in these environments. This possibly masks any large-scale factor associated with latitudinal gradient in trait diversity (i.e. an expected high functional redundancy among species in tropical region); and this is also true for continental shelf environment. We recognize the potential limitations of our approach, especially with regard to the taxonomic resolution used. Anyway, our study is the first to describe levels of functional redundancy in polychaete assemblages of distinct environments in the southwestern Atlantic. Future descriptive and experimental studies can take advantage of our results for a better understanding of functional redundancy patterns in tropical regions.

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Table S1. Morphological traits of polychaetes recorded in continental shelf and estuarine environments (PH.ab= absent; PH.ve= ventral; PH.am= axial muscular; PH.nm= axial non-muscular; JA.ab= absent; JA.pr= present; FS.ab= absent; FS.ss= a single structure; FS.ps= a pair of structures; FS.ms= multiple structures; SA.ab= absent; SA.os= only one structure; SA.ms= multiple structures; BA.ab= absent; BA.pr= present; CP.ab= all parapodial features absent; CP.us= parapodia uniramous simple; CP.uh= parapodia uniramous with uncini or hook; CP.bs= parapodia biramous simple; CP.bh= parapodia biramous with uncini or hook; BR.ab= absent; BR.re= regionalized; BR.nr= non-regionalized; BO.re= regionalized; BO.nr= non-regionalized; SE.100= ≤ 100 segments; SE.200= ≥ 101segments). *taxa exclusive of continental shelf environment; **taxa exclusive of estuarine environment.

Family	Morphological trait								
	Pharynx complexity	**Jaws presence**	**Feeding structures**	**Sensory appendages**	**Body appendages**	**Chaetal (parapodia) pattern**	**Branchiae regionalization**	**Body regionalization**	**Body size**
*Acoetidae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.us	BR.ab	BO.nr	SE.100
*Acrocirridae	PH.ve	JA.ab	FS.ps	SA.os	BA.ab	CP.bs	BR.re	BO.nr	SE.200
*Alciopidae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.us	BR.ab	BO.nr	SE.200
Ampharetidae	PH.ve	JA.ab	FS.ms	SA.ab	BA.ab	CP.bh	BR.re	BO.re	SE.100
Amphinomidae	PH.ve	JA.ab	FS.ps	SA.ms	BA.pr	CP.bs	BR.nr	BO.nr	SE.200
*Aphroditidae	PH.am	JA.pr	FS.ps	SA.os	BA.pr	CP.bs	BR.re	BO.nr	SE.100
**Apistobranchidae	PH.am	JA.ab	FS.ps	SA.ab	BA.pr	CP.bs	BR.nr	BO.nr	SE.100
*Arenicolidae	PH.nm	JA.ab	FS.ab	SA.ab	BA.ab	CP.bh	BR.re	BO.re	SE.100
Capitellidae	PH.nm	JA.ab	FS.ab	SA.ab	BA.ab	CP.uh	BR.ab	BO.nr	SE.100
Chaetopteridae	PH.ve	JA.ab	FS.ps	SA.ab	BA.ab	CP.bs	BR.ab	BO.re	SE.100

Chrysopetalidae	PH.am	JA.ab	FS.ps	SA.ms	BA.pr	CP.bs	BR.ab	BO.re	SE.100
Cirratulidae	PH.ve	JA.ab	FS.ps	SA.os	BA.ab	CP.bh	BR.nr	BO.nr	SE.200
Cossuridae	PH.am	JA.ab	FS.ss	SA.ab	BA.ab	CP.bs	BR.re	BO.re	SE.100
*Ctenodrilidae	PH.ve	JA.ab	FS.ab	SA.ab	BA.ab	CP.ab	BR.ab	BO.nr	SE.100
*Dinophilidae	PH.ve	JA.ab	FS.ab	SA.ab	BA.ab	CP.ab	BR.ab	BO.nr	SE.100
Dorvilleidae	PH.ve	JA.pr	FS.ps	SA.ms	BA.ab	CP.bs	BR.nr	BO.re	SE.200
Eulepethidae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.bs	BR.re	BO.nr	SE.100
Eunicidae	PH.ve	JA.pr	FS.ps	SA.ms	BA.pr	CP.bs	BR.nr	BO.nr	SE.200
*Euphrosinidae	PH.ve	JA.ab	FS.ab	SA.ms	BA.pr	CP.bs	BR.nr	BO.nr	SE.200
Fabriciidae	PH.ab	JA.ab	FS.ms	SA.os	BA.ab	CP.uh	BR.re	BO.re	SE.100
*Fauveliopsidae	PH.ab	JA.ab	FS.ab	SA.ab	BA.ab	CP.bs	BR.re	BO.nr	SE.100
Flabelligeridae	PH.ve	JA.ab	FS.ps	SA.os	BA.ab	CP.bs	BR.re	BO.nr	SE.100
Glyceridae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.bs	BR.ab	BO.nr	SE.200
Goniadidae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.bs	BR.ab	BO.nr	SE.200
Hesionidae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.bs	BR.ab	BO.nr	SE.100
**Histriobdellidae	PH.ve	JA.pr	FS.ps	SA.ms	BA.pr	CP.ab	BR.ab	BO.nr	SE.200
Iospilidae	PH.am	JA.pr	FS.ps	SA.os	BA.pr	CP.us	BR.ab	BO.nr	SE.200
**Longosomatidae	PH.ve	JA.ab	FS.ps	BA.ab	BA.pr	CP.bh	BR.re	BO.re	SE.200
*Lopadorrhynchidae	PH.am	JA.ab	FS.ps	SA.ms	BA.pr	CP.us	BR.ab	BO.nr	SE.200
Lumbrineridae	PH.ve	JA.pr	FS.ab	SA.ab	BA.pr	CP.bh	BR.ab	BO.nr	SE.200
Magelonidae	PH.ve	JA.ab	FS.ps	SA.ab	BA.ab	CP.bh	BR.ab	BO.re	SE.200
Maldanidae	PH.nm	JA.ab	FS.ab	SA.ab	BA.ab	CP.bs	BR.ab	BO.nr	SE.100
Nephtyidae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.bs	BR.nr	BO.nr	SE.200
Nereididae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.bs	BR.ab	BO.nr	SE.200
Oenonidae	PH.ve	JA.pr	FS.ab	SA.ab	BA.pr	CP.bs	BR.ab	BO.nr	SE.200
Onuphidae	PH.ve	JA.pr	FS.ms	SA.ms	BA.pr	CP.bh	BR.nr	BO.nr	SE.200
Opheliidae	PH.nm	JA.ab	FS.ab	SA.ab	BA.pr	CP.bs	BR.nr	BO.re	SE.100

Orbiniidae	PH.nm	JA.ab	FS.ab	SA.ab	BA.ab	CP.bs	BR.re	BO.nr	SE.100
Oweniidae	PH.ve	JA.ab	FS.ms	SA.os	BA.ab	CP.bh	BR.ab	BO.nr	SE.100
*Paralacydoniidae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.us	BR.ab	BO.nr	SE.200
Paraonidae	PH.nm	JA.ab	FS.ab	SA.os	BA.pr	CP.bs	BR.re	BO.nr	SE.200
Pectinariidae	PH.ve	JA.ab	FS.ms	SA.os	BA.pr	CP.bh	BR.re	BO.re	SE.100
Pholoidae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.bs	BR.nr	BO.nr	SE.100
Phyllodocidae	PH.am	JA.ab	FS.ps	SA.ms	BA.pr	CP.us	BR.ab	BO.nr	SE.200
Pilargidae	PH.am	JA.ab	FS.ps	SA.ms	BA.pr	CP.bs	BR.nr	BO.nr	SE.100
Poecilochaetidae	PH.ve	JA.ab	FS.ps	SA.os	BA.ab	CP.bs	BR.nr	BO.re	SE.200
Polygordiidae	PH.ve	JA.ab	FS.ps	SA.os	BA.ab	CP.ab	BR.ab	BO.nr	SE.200
Polynoidae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.us	BR.ab	BO.nr	SE.100
Protodrilidae	PH.ve	JA.ab	FS.ps	SA.ms	BA.pr	CP.ab	BR.ab	BO.nr	SE.100
*Protodriloididae	PH.ve	JA.ab	FS.ps	SA.ab	BA.pr	CP.ab	BR.ab	BO.nr	SE.200
Sabellariidae	PH.ab	JA.ab	FS.ps	SA.os	BA.pr	CP.uh	BR.re	BO.re	SE.100
Sabellidae	PH.ab	JA.ab	FS.ms	SA.os	BA.pr	CP.uh	BR.re	BO.re	SE.100
Saccocirridae	PH.ve	JA.ab	FS.ps	SA.ms	BA.pr	CP.us	BR.ab	BO.nr	SE.200
*Scalibregmatidae	PH.nm	JA.ab	FS.ab	SA.ab	BA.ab	CP.bs	BR.nr	BO.re	SE.200
Serpulidae	PH.ab	JA.ab	FS.ms	SA.os	BA.ab	CP.uh	BR.re	BO.re	SE.100
Sigalionidae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.bs	BR.nr	BO.nr	SE.200
*Sphaerodoridae	PH.am	JA.ab	FS.ps	SA.ms	BA.pr	CP.us	BR.ab	BO.nr	SE.200
Spionidae	PH.nm	JA.ab	FS.ps	SA.os	BA.pr	CP.uh	BR.nr	BO.nr	SE.100
Sternaspidae	PH.nm	JA.ab	FS.ab	SA.ab	BA.ab	CP.uh	BR.re	BO.nr	SE.100
Syllidae	PH.am	JA.ab	FS.ps	SA.ms	BA.pr	CP.us	BR.ab	BO.nr	SE.200
Terebellidae	PH.ve	JA.ab	FS.ms	SA.os	BA.pr	CP.bh	BR.re	BO.re	SE.200
*Tomopteridae	PH.am	JA.ab	FS.ps	SA.ms	BA.pr	CP.bs	BR.ab	BO.nr	SE.200
Trichobranchidae	PH.ve	JA.ab	FS.ms	SA.os	BA.pr	CP.bh	BR.re	BO.re	SE.200
*Typhloscolecidae	PH.am	JA.ab	FS.ab	SA.ab	BA.pr	CP.us	BR.ab	BO.nr	SE.200

Table S2. Functional entities (FEs) of the polychaetes families recorded in continental shelf and estuarine environments (the codes are found in Table 1 and Table A1).

Functional entities (i.e. unique combinations of the nine morphological traits evaluated)	ID	Taxa with this traits combination	Families per FE	
			Continental shelf	Estuarine
PHam_JApr_FSps_SAms_BApr_CPus_BRab_BOnr_ SE.100	FE1	Acoetidae, Polynoidae	2	1
PHvp_JAab_FSps_SAos_BAab_CPbs_BRre_BOnr_SE.200	FE2	Acrocirridae	1	0
PHam_JApr_FSps_SAms_BApr_CPus_BRab_BOnr_SE.200	FE3	Alciopidae, Paralacydoniidae	2	0
PHvp_JAab_FSms_SAab_BAab_CPbo_BRre_BOre_SE.100	FE4	Ampharetidae	1	1
PHvp_JAab_FSps_SAms_BApr_CPbs_BRnr_BOnr_SE.200	FE5	Amphinomidae	1	1
PHam_JApr_FSps_SAos_BApr_CPbs_BRre_BOnr_SE.100	FE6	Aphroditidae	1	0
PHnm_JAab_FSab_SAab_BAab_CPbo_BRre_BOre_SE.100	FE7	Arenicolidae	1	0
PHam_JAab_FSps_SAab_BApr_CPbs_BRnr_BOnr_SE.100	FE8	Apistobranchidae	0	1
PHnm_JAab_FSab_SAab_BAab_CPuo_BRab_BOnr_SE.100	FE9	Capitellidae	1	1
PHvp_JAab_FSps_SAab_BAab_CPbs_BRab_BOre_SE.100	FE10	Chaetopteridae	1	1
PHam_JAab_FSps_SAms_BApr_CPbs_BRab_BOre_SE.100	FE11	Chrysopetalidae	1	1
PHvp_JAab_FSps_SAos_BAab_CPbo_BRnr_BOnr_SE.200	FE12	Cirratulidae	1	1
PHam_JAab_FSss_SAab_BAab_CPbs_BRre_BOre_SE.100	FE13	Cossuridae	1	1
PHvp_JAab_FSab_SAab_BAab_CPab_BRab_BOnr_SE.100	FE14	Ctenodrilidae, Dinophilidae	2	0
PHvp_JApr_FSps_SAms_BAab_CPbs_BRnr_BOre_SE.200	FE15	Dorvilleidae	1	1

PHam_JApr_FSps_SAms_BApr_CPbs_BRre_BOnr_SE.100	FE16	Eulepethidae	1	1
PHvp_JApr_FSps_SAms_BApr_CPbs_BRnr_BOnr_SE.200	FE17	Eunicidae	1	1
PHvp_JAab_FSab_SAms_BApr_CPbs_BRnr_BOnr_SE.200	FE18	Euphrosinidae	1	0
PHab_JAab_FSms_SAos_BAab_CPuo_BRre_BOre_SE.100	FE19	Fabriciidae, Serpulidae	2	2
PHab_JAab_FSab_SAab_BAab_CPbs_BRre_BOnr_SE.100	FE20	Fauveliopsidae	1	0
PHvp_JAab_FSps_SAos_BAab_CPbs_BRre_BOnr_SE.100	FE21	Flabelligeridae	1	1
PHam_JApr_FSps_SAms_BApr_CPbs_BRab_BOnr_SE.200	FE22	Glyceridae, Goniadidae, Nereididae	3	3
PHam_JApr_FSps_SAms_BApr_CPbs_BRab_BOnr_SE.100	FE23	Hesionidae	1	1
PHvp_JApr_FSps_SAms_BApr_CPab_BRab_BOnr_SE.200	FE24	Histriobdellidae	0	1
PHam_JApr_FSps_SAos_BApr_CPus_BRab_BOnr_SE.200	FE25	Iospilidae	1	1
PHvp_JAab_FSps_SAab_BApr_CPbo_BRre_BOre_SE.200	FE26	Longosomatidae	0	1
PHam_JAab_FSps_SAms_BApr_CPus_BRab_BOnr_SE.200	FE27	Lopadorrhynchidae, Phyllodocidae, Sphaerodoridae, Syllidae	4	2
PHvp_JApr_FSab_SAab_BApr_CPbo_BRab_BOnr_SE.200	FE28	Lumbrineridae	1	1
PHvp_JAab_FSps_SAab_BAab_CPbo_BRab_BOre_SE.200	FE29	Magelonidae	1	1
PHnm_JAab_FSab_SAab_BAab_CPbs_BRab_BOnr_SE.100	FE30	Maldanidae	1	1
PHam_JApr_FSps_SAms_BApr_CPbs_BRnr_BOnr_SE.200	FE31	Nephtyidae, Sigalionidae	2	2
PHvp_JApr_FSab_SAab_BApr_CPbs_BRab_BOnr_SE.200	FE32	Oenonidae	1	1
PHvp_JApr_FSms_SAms_BApr_CPbo_BRnr_BOnr_SE.200	FE33	Onuphidae	1	1
PHnm_JAab_FSab_SAab_BApr_CPbs_BRnr_BOre_SE.100	FE34	Opheliidae	1	1
PHnm_JAab_FSab_SAab_BAab_CPbs_BRre_BOnr_SE.100	FE35	Orbiniidae	1	1
PHvp_JAab_FSms_SAos_BAab_CPbo_BRab_BOnr_SE.100	FE36	Oweniidae	1	1

PHnm_JAab_FSab_SAos_BApr_CPbs_BRre_BOnr_SE.200	FE37	Paraonidae	1	1
PHvp_JAab_FSms_SAos_BApr_CPbo_BRre_BOre_SE.100	FE38	Pectinariidae	1	1
PHam_JApr_FSps_SAms_BApr_CPbs_BRnr_BOnr_SE.100	FE39	Pholoidae	1	1
PHam_JAab_FSps_SAms_BApr_CPbs_BRnr_BOnr_SE.100	FE40	Pilargidae	1	1
PHvp_JAab_FSps_SAos_BAab_CPbs_BRnr_BOre_SE.200	FE41	Poecilochaetidae	1	1
PHvp_JAab_FSps_SAos_BAab_CPab_BRab_BOnr_SE.200	FE42	Polygordiidae	1	1
PHvp_JAab_FSps_SAms_BApr_CPab_BRab_BOnr_SE.100	FE43	Protodrilidae	1	1
PHvp_JAab_FSps_SAab_BApr_CPab_BRab_BOnr_SE.200	FE44	Protodriloididae	1	0
PHab_JAab_FSps_SAos_BApr_CPuo_BRre_BOre_SE.100	FE45	Sabellariidae	1	1
PHab_JAab_FSms_SAos_BApr_CPuo_BRre_BOre_SE.100	FE46	Sabellidae	1	1
PHvp_JAab_FSps_SAms_BApr_CPus_BRab_BOnr_SE.200	FE47	Saccocirridae	1	1
PHnm_JAab_FSab_SAab_BAab_CPbs_BRnr_BOre_SE.200	FE48	Scalibregmatidae	1	0
PHnm_JAab_FSps_SAos_BApr_CPuo_BRnr_BOnr_SE.100	FE49	Spionidae	1	1
PHnm_JAab_FSab_SAab_BAab_CPuo_BRre_BOnr_SE.100	FE50	Sternaspidae	1	1
PHvp_JAab_FSms_SAos_BApr_CPbo_BRre_BOre_SE.200	FE51	Terebellidae, Trichobranchidae	2	2
PHam_JAab_FSps_SAms_BApr_CPbs_BRab_BOnr_SE.200	FE52	Tomopteridae	1	0
PHam_JAab_FSab_SAab_BApr_CPus_BRab_BOnr_SE.200	FE53	Typhloscolecidae	1	0

Supplement S1. R script: packages and procedures employed to measure and analyze the functional redundancy of polychaetes assemblages.

```
#### Attaching the necessary packages to run the functions and
analyzes
library(FD)
library(vegan)
library(cluster)
library(ade4)
library(ape)
library(geometry)

#### Loading general data
spe<-read.table("spe.txt", sep=";", header=T, row.names=1)
#species occurrences
traits<-read.table("traits.txt", sep=";", header=T, row.names=1)
#species functional traits

#### species_to_fe function
species_to_FE<-function(x){
  if ( nrow(traits)<2 ) stop("Error: 'traits' should have at
least 2 rows")
  if ( ncol(traits)<2 ) stop("Error: 'traits' should have at
least 2 columns")
  for ( t in names(traits) )
  {
    if ( is.numeric(traits[,t]) ) stop( paste("Error: trait
'",t,"' is coded as 'numeric' ", sep="") )
    if( sum(is.na((traits[,t])))>0 ) stop(paste("Error: NA in
trait '",t,"' ", sep=""))
  }
  traits_codes<-substr(names(traits),1,1)
  if ( length(unique(traits_codes))!=ncol(traits) ) {
    traits_codes<-substr(names(traits),1,2)
    if ( length(unique(traits_codes))!=ncol(traits) )
stop("Error: 2 first letters of trait names should be unique ")
  }
  names(traits_codes)<-names(traits)
  for ( t in names(traits) )
  {
    mod_t<-unique(traits[,t])
    if ( length(unique(substr(mod_t,1,2)))!=length(mod_t) )
stop( paste("Error: some levels of trait '",t,"' have the same 2
first letters", sep="") )
  }
  FE<-paste( toupper(traits_codes[1]),
tolower(substr(traits[,1], 1,2) ) ,sep="") #defining FEs as
unique combinations of trait values
```

```
  for (t in names(traits)[-1] )
  {
    FE<-paste( FE, paste( toupper(traits_codes[t]),
tolower(substr(traits[,t], 1,2) ) ,sep="") , sep="_")
  }
  names(FE)<-row.names(traits)
  FE_codes<-unique(FE) #codes of FE
  FE_sp_01<-matrix(0, length(FE_codes), nrow(traits),
dimnames=list( FE_codes, row.names(traits) ) ) # matrix of
species occurence in FE
  for (f in FE_codes)
  {
    FE_sp_01[f,names(which(FE==f))]<-1
  }
  FE_traits<-traits[apply(FE_sp_01, 1, function(x)
{names(which(x==1))[1]} ), ] #trait values for FE
  row.names(FE_traits)<-row.names(FE_sp_01)
  res<-list( FE=FE, FE_codes=FE_codes, FE_sp_01=FE_sp_01,
FE_traits=FE_traits) #results in a single list
  return(res)
} #end of function
```

PCoA with presence/absence data of families in functional entities

```
FEs<-read.table("FEs.txt", sep=";", header=T, row.names=1)
#loading the presence/absence data of families in functional
entities
jaccard.FEs<-vegdist(FEs,'jaccard') #transforming the original
data matrix into a Jaccard distance matrix
pcoa.FEs<-pcoa(jaccard.FEs)
summary(pcoa.FEs)
```

Multidimensional functional space on the basis of the species traits

```
traits.diss<-daisy(traits, metric = "gower")
traits.pcoa<-pcoa(traits.diss, correction="cailliez")
traits1<-traits.pcoa$vectors[,1:3] #select the 3 first axis of
the PCoA
```

Functional originality (FOri) and functional uniqueness (FUni) - according to Buisson et al. (2013), Maire et al. (2013), Mouillot et al. (2013)

```
T<-dim(traits1)[3] #T = number of axis
# definition of the vector for results, with species' names as
given in 'spe'
N<-nrow(spe)
FOri<-rep(NA,N) ; names(FOri)<-row.names(spe)
FUni<-rep(NA,N) ; names(FUni)<-row.names(spe)
```

```
# scaling and centering of each trait according to all species
values
traitsSC<-scale(traits1, center=TRUE, scale=TRUE)
# functional specialization of each species (distance to point
0,0 in the standardized functional space)
FOriS <- (apply(traits1, 1, function(x) {x%*%x} ) )^0.5
FOriS <- FOriS/max(FOriS)
# functional originality and functional uniqueness of each
species (distance to point nearest neighbour in the standardized
functional space)
dist_Uni = as.matrix(dist(traits1, method="eucl"))
FUniS = vector()
for (j in 1:nrow(dist_Uni))
{
  FUniS[j] = min(dist_Uni[-j,j])
}
FUniS2=FUniS/(max(FUniS))
# computation of the two indices site by site
for (i in 1:nrow(spe)) ## a loop for all sites (row of the
faunistic table)
{
  if (length(which(spe[i,]>0))>0) ## we exclude the site without
species and give them a 0-value in the 'else' below
  {
    ## FOri
    # mean functional specialization in the communities
    FOri[i]<-
as.numeric(spe[i,]/sum(spe[i,]))%*%as.numeric(FOriS)
    ## FUni
    # mean functional originality in the communities according
to the full pool of species
    FUni[i] <-
as.numeric(spe[i,]/sum(spe[i,]))%*%as.numeric(FUniS2)
  }
  else
  {
    FOri[i] <- 0
    FUni[i] <- 0
  }
} #end of function
# the value by species can be extracted from FOriS and FUniS2
func_species<-data.frame(SP=colnames(spe), SP_FOri=FOriS,
SP_FUni=FUniS2)
print(func_species)
```

Kruskal-Wallis non-parametrit test

```
fori_funi<-read.table("fori_funi.txt",header=T) #loading the
data with the FOri and FUni values measured for each environment
```

```
kruskal1<-kruskal.test(FOri~environment, data=fori_funi)
kruskal2<-kruskal.test(FUni~environment, data=fori_funi)
```

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CONSIDERAÇÕES FINAIS

No primeiro capítulo, por meio de uma revisão teórica, mostrei que há diversos métodos disponíveis para avaliar a função macrobêntica em ambientes costeiros (e.g., índices bióticos, índices de diversidade funcional uni e multivariados, e análise de atributos biológicos). No entanto, apesar da evidente aplicabilidade dessas abordagens para avaliação da relação entre as características das espécies e o funcionamento dos ecossistemas, é preciso cautela para sua ampla utilização. Cada técnica traz vantagens e limitações que precisam ser consideradas para sua eventual validação. Também observei que a clara falta de evidências empíricas dos atributos funcionais e a falta de padronização de terminologias e protocolos dificultam que os métodos sejam usados de forma objetiva. Ainda assim, a utilização combinada das abordagens (como por exemplo, a análise de atributos biológicos e de índices de diversidade funcional) representa um caminho promissor para descrever e avaliar a estrutura das comunidades bênticas.

No segundo capítulo, encontrei que nitrogênio total e o tamanho médio dos grãos são as variáveis que melhor explicam a diversidade funcional de poliquetas estuarinos ao longo da costa sul e sudeste do Brasil. O conteúdo orgânico dos sedimentos, expresso pelo nitrogênio total, fósforo total, carbono total e matéria orgânica, influenciou sobretudo a composição funcional, associando atributos específicos a processos ecológicos que podem ser diretamente relacionados a esses parâmetros, como ciclagem de nutrientes, produção secundária e fluxo de energia. Além disso, observei baixos valores de diversidade funcional nos estuários, consequência dos táxons numericamente dominantes que ocorrem frequentemente nesses sistemas e que compartilham uma elevada quantidade de atributos funcionais.

No terceiro capítulo, verifiquei que, de maneira geral, as assembleias de poliquetas em ambientes de plataforma e estuarinos do *South Brazil Shelf Large Marine Ecosystem (SBSLME)* apresentam baixa redundância funcional. Também inferi que níveis mais altos de redundância em ambientes estuarinos são impostos pelas forçantes ambientais que atuam nesses sistemas e conduzem as assembleias a uma maior convergência evolutiva (i.e., maior número de táxons compartilhando os mesmos atributos funcionais e desempenhando funções ecológicas semelhantes). Finalmente, concluí que embora os poliquetas estuarinos tenham menos combinações únicas de atributos funcionais, as combinações são mais originais e mais adequadas para lidar com as condições ambientais extremamente variáveis nesses ambientes.

O trabalho da tese como um todo evidencia que a escolha adequada da medida de diversidade funcional – levando em conta suas vantagens e limitações, bem como os objetivos do estudo, hipóteses a serem testadas, grupo taxonômico utilizado, e atributos funcionais selecionados – é essencial para uma descrição mais rigorosa, mais replicável e mais útil de padrões gerais que possam ser extrapolados para outros contextos de estudo. Embora esta pareça ser uma obviedade metodológica, uma má escolha da técnica de mensuração, entre as muitas já disponíveis na literatura, pode afetar grandemente as conclusões dos trabalhos ecológicos. O uso da métrica apropriada pode fornecer resultados que de fato ajudem a entender os mecanismos que propiciam elevados ou baixos níveis de diversidade e redundância funcionais.

Finalmente, concluo que a investigação da diversidade funcional de assembleias bênticas merece ser aprofundada, pois pode resultar no efetivo reconhecimento de processos que alteram a biodiversidade do grupo e não são facilmente detectáveis a partir apenas da análise da diversidade taxonômica. Isso é particularmente verdadeiro para os ambientes marinhos costeiros, onde a crescente pressão antrópica tem alterado

de forma considerável o funcionamento dos ecossistemas e a sua capacidade de prover bens e serviços para populações humanas.

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